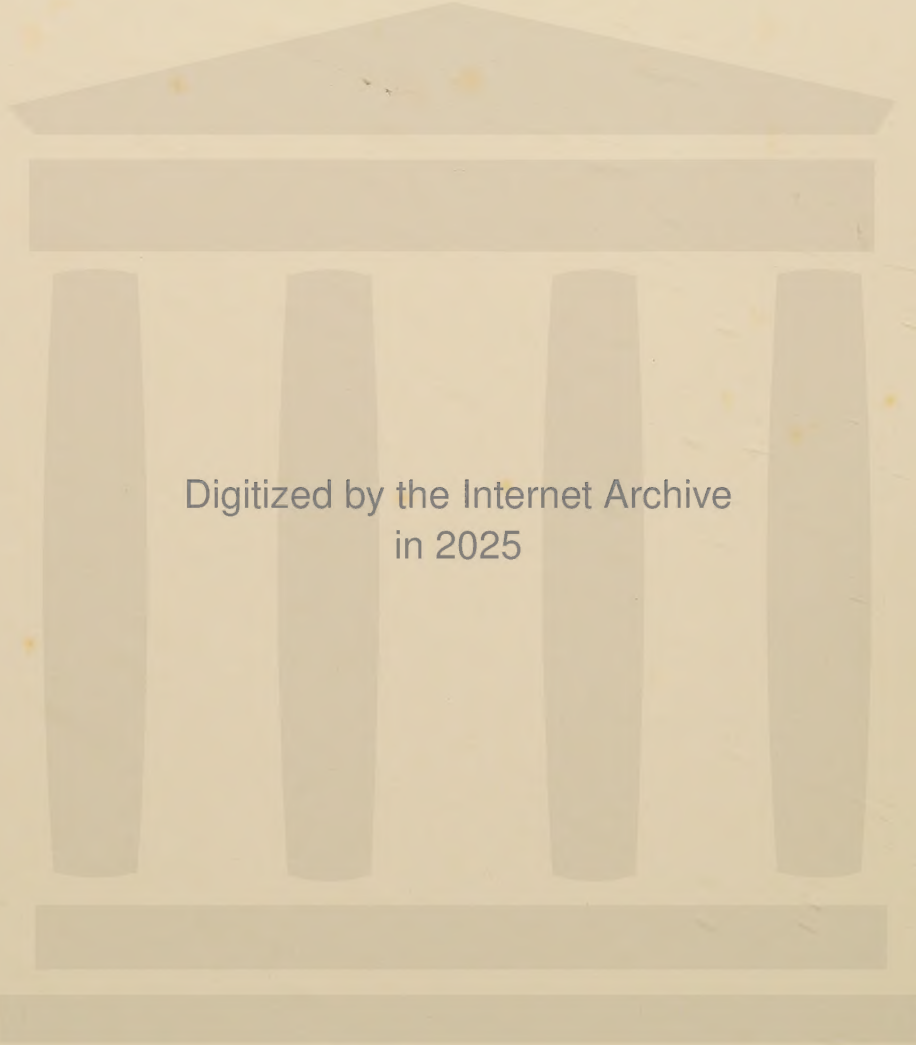


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FATTY ACIDS IN DEPOT FATS OF GREEN TURTLES *CHELONIA MYDAS* FROM THE HAWAIIAN ISLANDS AND JOHNSTON ATOLL

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Abstract—1. Depot fat samples from thirteen individual mid-Pacific turtles *Chelonia mydas* were examined for overall fatty acid composition.

2. It can be concluded from analysis of fatty acids that the mid-Pacific green turtles generally synthesize their triglyceride depot fats with at least one, but not more than two, positions occupied by 12:0 and 14:0, possibly with 16:0 and 16:1 as well.

3. These two fatty acids are probably utilized as temporary energy storage and are synthesized from acetate originating in the gut from dietary carbohydrates.

4. The most probable source of dietary carbohydrate is benthic algae. These, their epiphytes, and gut bacteria also contribute numerous minor and trace unsaturated fatty acids.

5. A select group of four oils of high iodine value (>100) are shown to have a higher than common concentration of 22:6n-3–22:5n-3. This suggests a particular dietary source of fatty acids different from the other samples, possibly including jellyfish or other animal matter.

INTRODUCTION

The marine turtles are a fascinating group of animals in some danger of disappearing (Thompson, 1988; Davenport *et al.*, 1990). Through energy conservation practices (Naito *et al.*, 1990; Sakamoto *et al.*, 1990) they are capable of extended migration over thousands of miles, presumably without food *en route* (Bustard, 1972). The fact that the bodies are therefore rich in oil has long been known but relatively little work on the composition of their oils (Hilditch and Williams, 1964) was possible until the development of gas-liquid chromatography. In the last three decades details on the fatty acids of depot fats for a considerable number of species have been published (Ackman *et al.*, 1971; Joseph *et al.*, 1985; Holland *et al.*, 1990).

In the western Atlantic, turtle grass *Thalassia testudinum* is a basic food of the green turtle *Chelonia mydas* (Bjorndal, 1980; Williams, 1988). The range of the green turtle includes the Pacific Ocean, where several sea-grasses are found (Nichols and Johns, 1985). However, in mid-Pacific these grasses are often scarce and alternative diets must be the norm. In an attempt to continue the *C. mydas* food chain observations published for Caribbean samples (Joseph *et al.*, 1985) we have examined green turtle depot fat samples from thirteen animals of the Hawaiian Islands and Johnston Atoll mid-Pacific region.

MATERIALS AND METHODS

Samples of freshly biopsied depot fats from field studies of *C. mydas* were tightly packed in glass vials and flown to Halifax, and stored frozen at -30°C until analyzed. The fat was dissolved in petroleum ether and the triglycerides purified by thin-layer chromatography on silica gel. Conversion of triglycerides to methyl esters with 7% BF₃-MeOH was followed by gas-liquid chromatography in a PE-8420 apparatus on a column of flexible fused silica with a bonded Carbowax-20M coating (SUPELCOWAX-10, 30 m $\times$ 0.25 mm i.d.). Operating conditions were: hold at 185°C for 8 min, program to 220°C at $1^{\circ}/\text{min}$, and hold, as described and illustrated by Ackman (1987). Peak areas were converted to weight per cent fatty acids by a program (Ackman and Eaton, 1978) incorporating flame ionization correction factors (Craske and Bannon, 1988) and simultaneously providing a calculated iodine value.

RESULTS

The fourteen analyses of triglycerides included one duplicate analysis (Table 1). Basically, all had four important saturated acids ranging in total from 37 (w/w)% to just over 50 (w/w)%. Similarly, monoethylenic acid totals ranged from 35 (w/w)% to 45 (w/w)%. There were few distinctive characteristics among the polyunsaturated fatty acids, but the calculation of (w/w)% fatty acids by the computer program also provided the calculated iodine value. This is a fair summation of the numbers of ethylenic bonds in all types of fats (Hilditch and Williams, 1964), including marine oils of fish and mammal origin (Ackman, 1982). Accordingly the samples of Table 1 are organized in descending order of calculated iodine

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Table 1. Fatty acids (w/w%) of depot fats of mid-Pacific green turtles with group designations and origins from Hawaii or Johnston Atoll

Sample nos.	Group I					Group II					Group III				
	6	11	2	10	13	5*	4*	9	15	7	3	8	12	14	
Geographical origin	HI	JA	HI	JA	JA	HI	HI	JA	JA	HI	HI	JA	JA	JA	
Fatty acid	tr	1.34	0.71	2.64	2.03	0.85	0.99	0.91	1.58	0.53	0.33	0.67	0.57	1.56	
10:0	6.60	6.56	10.93	10.09	13.17	16.78	18.05	16.02	16.04	13.18	11.17	20.32	20.67	17.54	
12:0	0.33	0.36	0.22	0.41	0.49	0.29	0.32	0.26	0.40	0.13	0.20	0.40	0.22	0.19	
13:0	6.98	5.86	7.83	6.87	9.26	9.25	9.31	10.17	10.74	9.75	11.06	11.45	11.97	11.55	
14:0	0.59	0.75	0.54	0.52	0.48	0.25	0.24	0.29	0.32	0.20	0.25	0.33	0.20	0.11	
16:0	0.36	0.21	0.17	0.19	0.20	0.09	0.08	0.12	0.10	0.08	0.07	0.08	0.07	tr	
16:1n-7	13.90	13.12	14.11	14.50	14.59	15.79	15.63	15.83	16.11	19.14	16.36	14.96	15.89	16.70	
17:0	1.11	0.95	0.65	0.65	0.54	0.28	0.26	0.36	0.30	0.11	0.82	0.23	0.20	0.24	
18:0	4.86	5.79	5.04	5.38	4.59	4.83	4.78	4.70	4.89	5.49	6.67	4.12	4.18	4.95	
20:0	1.87	0.54	0.50	0.70	0.37	0.09	0.09	0.31	0.17	0.10	0.21	0.08	0.09	0.09	
22:0	0.39	0.29	0.23	0.19	0.17	0.02	0.14	0.12	0.09	0.16	0.13	0.08	0.08	0.07	
Σ Saturates	36.99	35.77	40.93	42.14	45.89	48.52	50.09	49.09	50.74	48.87	47.27	52.54	54.11	53.19	
14:1n-5	0.38	0.39	0.49	0.46	0.60	0.56	0.57	0.72	0.69	0.62	0.61	0.75	0.77	0.69	
16:1n-7†	4.96	5.85	6.08	7.05	7.15	6.50	6.35	8.85	8.25	8.42	5.90	8.28	9.23	8.99	
16:1n-5	0.10	0.17	0.24	0.13	0.15	0.14	0.13	0.14	0.19	0.11	0.10	0.15	0.14	0.14	
18:1n-9	20.84	26.94	22.79	24.99	24.83	25.43	24.34	26.31	26.29	30.46	33.92	28.07	25.71	27.42	
18:1n-7	2.31	2.80	2.99	2.97	3.18	3.99	4.04	3.50	3.77	2.48	2.95	3.56	3.81	3.69	
18:1n-5	0.18	0.25	0.24	0.20	0.24	0.29	0.27	0.31	0.35	0.17	0.15	0.33	0.32	0.30	
20:1n-11	0.51	0.30	0.32	0.36	0.18	0.13	0.11	0.09	0.08	0.06	0.17	0.12	0.09	0.11	
20:1n-9	1.04	1.24	0.96	0.59	0.60	0.40	0.28	0.35	0.42	0.35	0.82	0.29	0.26	0.28	
20:1n-7	0.37	0.27	0.27	0.18	0.14	0.10	0.09	0.12	0.14	0.08	0.18	0.11	0.10	0.10	
22:1n-11, n-13	1.80	0.17	0.69	0.54	0.40	0.11	0.15	0.29	0.16	0.21	0.21	0.11	0.11	0.11	
22:1n-9	0.65	0.59	0.33	0.23	0.22	0.19	tr	0.16	0.09	0.38	0.12	0.07	0.09	0.06	
24:1	2.61	0.73	0.98	0.82	0.57	0.32	0.49	0.30	0.20	0.57	0.38	0.15	0.17	0.14	
Σ Monoenes	35.75	39.70	36.38	38.52	38.28	38.16	36.82	41.14	40.63	43.91	45.51	41.99	40.80	42.03	
16:2n-7	1.02	0.67	0.53	0.68	0.44	0.08	0.15	0.29	0.15	0.15	0.08	0.20	0.08	0.09	
18:2n-6	0.54	0.61	0.63	0.54	0.37	0.97	0.90	0.24	0.26	0.39	0.24	0.16	0.14	0.14	
18:2n-4	0.23	0.37	0.25	0.23	0.23	0.34	0.30	0.15	0.18	0.24	0.03	0.21	0.11	0.18	
20:2n-10	0.10	0.06	0.10	0.04	0.08	0.13	0.12	0.07	0.08	0.20	0.73	0.06	0.08	0.05	
20:2n-9	0.05	0.07	0.09	0.11	0.10	0.02	tr	0.13	0.16	0.02	0.14	0.05	0.20	0.17	
20:2n-6	0.33	0.38	0.32	0.25	0.20	0.21	0.19	0.19	0.18	0.20	0.16	0.19	0.20	0.18	
Σ Dienes	2.27	2.16	1.92	1.85	1.42	1.75	1.66	1.07	1.01	1.20	1.38	0.87	0.81	0.81	

Continued opposite

Table 1. *Continued*

Sample Nos.	Geographical origin	Fatty acid	Group I			Group II					Group III				
			6	11	2	10	13	5*	4*	9	15	7	3	8	14
16:3n-6			0.43	0.75	0.52	0.55	0.55	0.57	0.52	0.44	0.05	0.23	0.17	0.30	0.30
16:3n-3			0.46	0.52	0.28	0.30	0.21	0.20	0.21	0.11	0.14	0.28	tr	0.05	0.05
18:3n-6			0.12	0.14	0.11	0.12	0.07	tr	0.09	0.04	0.03	0.05	0.02	0.02	0.02
18:3n-4			tr	tr	tr	tr	tr	tr	tr	tr	tr	tr	tr	tr	tr
18:3n-3			0.19	0.28	0.34	0.21	0.19	1.37	1.29	0.14	0.21	0.36	tr	0.14	0.11
20:3n-9			0.02	tr	0.23	tr	0.18	tr	tr	0.03	0.02	tr	0.04	0.02	0.02
20:3n-6			0.09	0.17	0.11	0.16	0.32	0.35	0.31	0.13	0.13	0.26	0.31	0.14	0.10
20:3n-3			0.23	0.11	0.11	0.07	0.24	0.05	0.16	0.23	0.17	0.15	0.06	0.17	0.16
Σ Trienes			1.54	1.97	1.70	1.41	1.76	2.64	2.58	1.12	0.75	1.33	0.60	0.84	0.76
18:4n-3			0.22	0.19	0.21	0.24	0.14	0.50	0.51	0.11	0.10	0.09	0.04	0.07	0.06
18:4n-1			tr	tr	0.03	tr	0.01	0.01	tr	0.01	tr	tr	0.02	tr	tr
20:4n-6			0.74	1.68	1.47	1.35	0.98	1.16	1.11	0.71	0.80	1.08	0.42	0.52	0.37
20:4n-3			0.23	0.38	0.24	0.31	0.25	0.43	0.40	0.18	0.12	0.13	0.14	0.13	0.10
22:4n-6			1.66	1.60	2.02	1.16	1.07	0.60	0.70	0.38	0.39	0.38	0.93	0.28	0.30
22:4n-3			0.23	0.10	0.12	0.08	0.09	0.12	0.11	0.08	0.06	0.11	0.09	0.06	0.04
Σ Tetraenes			3.08	3.95	4.09	3.14	2.54	2.82	2.83	1.47	1.47	1.79	1.64	1.06	0.77
20:5n-3			0.39	1.24	1.04	1.48	1.17	1.60	1.63	1.20	1.05	0.92	0.27	0.73	0.49
21:5n-3			0.15	0.15	0.13	tr	tr	0.14	0.13	tr	tr	0.21	0.49	0.16	tr
22:5n-6			1.96	1.60	1.61	0.89	0.68	0.22	0.32	0.32	0.43	0.18	0.10	0.10	0.11
22:5n-3			3.71	2.57	2.65	2.10	1.99	2.95	2.83	1.60	1.31	1.18	1.65	1.15	0.71
Σ Pentaenes			6.21	5.56	5.43	4.47	3.84	4.88	4.81	3.12	2.79	2.49	2.51	2.14	1.31
22:6n-3			13.63	10.24	9.07	7.91	4.79	0.77	0.81	2.29	1.56	0.50	0.37	0.30	0.35
Iodine value			131.49	122.54	112.72	102.74	86.88	74.31	72.72	68.60	63.11	61.17	59.57	53.44	50.52

*Same animal.

†Includes *trans*-6-hexadecenoic acid (Ackman *et al.*, 1971).

value and are divided arbitrarily into three groups for discussion purposes. Samples with numbers 8-14 were collected at Johnston Atoll but this does not bias the assignment by calculated iodine value, some falling into each group. The four turtle oils with iodine values of 131-103 (Group I) are in the low range for fish oils, but comparable to some herring oils (Ackman and Eaton, 1970). However, in many fish oils the "basic composition" of fish oils (Ackman *et al.*, 1988) is modified by two exogenous long-chain monoethylenic fatty acids, usually with 22:1 > 20:1. The Group I mid-Pacific turtle oils actually contained slightly more saturated fatty acids than marine fish oils which can often have up to 30% of such acids (Ackman, 1988). The four Group I oils have 16:0 (palmitic acid) and 14:0 (myristic acid) represented in about the same proportions, 13-14%, and 6-11% respectively, as are found in most fish oils (Ackman, 1982), but there is about 5% stearic acid in the turtle oils vs about 1% in most fish oils. A second and definitely a key factor differentiating the turtle total saturated acids from those of fish oils is the 12:0 (lauric acid) present in proportions as high as 11%. This acid is present only in traces in fish oils.

The monoethylenic fatty acids in the turtle oils are dominated by the ubiquitous 18:1n-9 (oleic) acid, accompanied by the 18:1n-7 isomer (*cis*-vaccenic acid) in a 10:1 proportion. In clupeid fish oils, which are rich in 22:1, the 22:1n-11 isomer (cetolic acid) is of exogenous origin (Ackman *et al.*, 1980) and dominant. In the turtle fats the 22:1n-9 (erucic acid) isomer is about as important, and is potentially of endogenous origin, as is the 16:1n-7 (palmitoleic acid). In this group the dienoic and trienoic polyunsaturated fatty acids are all minor, as is also not unusual in marine fish oils. The tetraenoic acids show enrichment in both 20:4n-6 (arachidonic acid) and the higher homologue 22:4n-6 (adrenic acid). The 20:4n-6 is about three to four times as important as in clupeid fish oils, and the equally obvious 22:4n-6 is about 10 times as important as in the fish oils. These two fatty acids are an indication of the tropical fatty acid systems which are notably richer in these two fatty acids than the northerly (or southerly) fish oil and lipid fatty acids (Ackman, 1989). This feature extends into the pentaenoic acids where 22:5n-6, also a minor fatty acid in clupeid oils, is almost as important as the other pentaenoic acid, the isomeric 22:5n-3. The latter is also the isomer found in high proportions in cold water seal oils (Ackman and Eaton, 1988). The surprising feature of the four Group I oils is however the high (8-14%) proportion of 22:6n-3 (docosahexaenoic acid or DHA). As this fatty acid has an iodine value of 464, it is clear that it is a major factor in the high iodine value of this group of turtle fats.

The second group (II) of four turtle fat analyses represents only three animals (see below). The iodine values ranging from 87 down to 69, have no exact parallel in commercial fish oils, although a crab triglyceride fraction of comparable iodine value has been described (Takeuchi and Ackman, 1987). This group of animals shows a moderate increase in total saturated fatty acids to 50% and this increase is mostly in 12:0, which approximately doubles to as

much as 16%, and in 14:0 which increases by about 50%. Stearic acid (18:0) is, however, the same percentage of total fatty acids as in the fatty acids of the higher iodine value group.

The monoethylenic fatty acid totals change very little, but 20:1 and 22:1 are reduced overall. An unexpected change is in the proportion of 18:1n-7 to 18:1n-9, the former increasing from an average of 10.4% of total 18:1 for the first four oils to 12.7 for the second three animals with oils of lesser iodine values. This reflects an increase in the related 16:1n-7 from an average of 6% to 7.2%.

The dienoic, trienoic and tetraenoic polyunsaturated fatty acid are reduced by about 50% in these three animals compared to the high iodine value group. This extends to all of the higher unsaturated acids but principally affects the 22:6n-3, which drops to less than the 22:5n-3 in the one animal providing two of the four oils analyzed. These two samples, 5 (carapace) and 4 (pelvis), came from one animal and provide convincing evidence of the stability of the samples, the accuracy of the GLC analysis, and the uniformity of distribution of depot fat composition in these large animals. This animal has less 22:6n-3 than the other two in the group, but this is compensated for by the higher total pentaene fatty acids.

The last six oils (Group III) have iodine values from 63 down to 51. There is, however, no further increase of note in the saturated fatty acids which stabilize at almost exactly 50% by weight of fatty acids. Of this as much as 21% by weight is 12:0 and 12% is 14:0. The two highest 12:0 numbers may be offset by less 18:0 and possibly also by less 16:0.

In the monoethylenic acids the totals for Group III are consistently just over 40% of all fatty acids. With the exception of oils 7, and 3, and 12, the percentages of 18:1n-7 in total 18:1 average 12.15, or about the same as in Group II. The further increase in 16:1n-7 to an average of 8.2% is thus not reflected in chain extension to 18:1n-7. The 20:1 and 22:1 fatty acids are still definite components but not of any importance. The less polyunsaturated fatty acids are again negligible in importance, and there is a further drop in 22:6n-3 to well under 1% (except for No. 15), a major difference since the total pentaenes, especially 22:5n-3, remain higher.

DISCUSSION

To consider the implications of the fatty acids in the low iodine marine value oils of green turtles one must consider the proportions of fatty acids in mole per cent and not weight per cent. The approximately 50% weight percent of saturated acids includes, in round (w/w%) figures, 20% of 12:0, and 10% of 14:0. The lower molecular weight of these acids means that they add up to higher percentage numbers in mole %, and if combined with 16:0 and 16:1 the total mole % is at least 55, approaching two-thirds of the fatty acids. Thus two out of three glycerol positions could be occupied by those shorter-chain saturated fatty acids (plus 16:1) which have no obvious dietary source and can be readily biosynthesized by the turtles themselves (Joseph *et al.*, 1985). Litchfield (1972) has discussed the rather scanty data for fatty

acid distribution of turtle oil fatty acids in triglycerides as part of a review of specific synthesis of triglycerides. The dearth of polyunsaturated fatty acids in the six particularly low iodine value oils of Group III, means that the turtles are forced to use freshly biosynthesized monoethylenic fatty acids to make up the balance of the triglyceride fatty acids since polyunsaturated fatty acids require at the least C_{18} precursors. The small increase in 16:1n-7 may be included in this process but both of the necessary 16:1n-7 and 18:1n-9 could be either dietary or biosynthesized *de novo*. Brockerhoff *et al.* (1968) clearly show the 16:1 and 18:1 concentrated in the 2-position for triglycerides of the leatherback *Dermochelys coriacea coriacea*. The saturated acids 12:0, 14:0, 16:0 and 18:0 in the same sample (Table 2) have a rather peculiar distribution. The two shorter chains are equitably distributed in the 1,3-positions, but the two longer chains favor the 1-position, over the 3-position, as in other higher animals. Litchfield did not clarify the status of the pentaenoic acids in the few turtle triglycerides examined.

The four high iodine value oils contain approximately one-third mole per cent for the three principal saturated fatty acids (12:0 + 14:0 + 16:0). It thus appears possible to speculate that the triglycerides of the green turtle depot fats always contain at least one-third freshly biosynthesized saturated acids in the 1- and 3-position (Table 2).

There are two possible reasons for this emphasis on shorter chain saturated fatty acids. One is the need for a low-melting depot fat which could be favored by a mixture of fatty acids rich in 12:0. The large marine turtle body temperatures may well be higher than that of the ambient sea-water as discussed elsewhere (Ackman *et al.*, 1971; Frair *et al.*, 1972; Davenport *et al.*, 1990; Holland *et al.*, 1990). The second is that this is a simple way of storing energy from dietary carbohydrate.

Stomach contents and observations of feeding behaviour of mid-Pacific green turtles (Balazs, 1985; Balazs *et al.*, 1987) have recently been published. If the diet of the Pacific green turtle is basically benthic algae but occasionally includes sea-grasses, coelenterates, or floating algae, or fish remains, then all of the polyunsaturated acids, including the 20:4n-6 and 22:4n-6 (Sipos and Ackman, 1968; Arai *et al.*, 1989; Holland *et al.*, 1990), are explained and the basic triglyceride simply incorporates these from the diet without modification. One piece of evidence suggesting a particular diet factor for this group is the ratio of 22:6n-3 to 22:5n-3. For samples 6, 11, 2 and 10 this figure is 3.7, 4.0, 3.4 and 3.8. In the other groups there is no such correlation, but the low levels preclude a definitive comparison. Bjorndal *et al.* (1991) discuss why green turtles may select a specific

diet. Litchfield (1972) speculated that the position on the glycerol of the n-3 pentaenoic acid in the one marine turtle triglyceride examined would be similar to that of the 22:6n-3.

Whatever the origin, it is clear from the accumulations of long-chain fatty acids of both the n-6 and n-3 families (Table 1) that there is no $\Delta 4,5$ desaturase. This would be necessary to extend these fatty acids respectively to 22:5n-6 and 22:6n-3 (Chapkin and Miller, 1990; Cleland *et al.*, 1990; Garcia *et al.*, 1990). If operative on 22:5n-3 it should, according to current thinking, be equally operative in 22:4n-6, which is not the case. Depot fats need to be distinguished from meat lipids which contain phospholipids, but Alian *et al.* (1986) have observed that green turtle "meat contained less unsaturated fatty acid than loggerhead turtle meat". This could be the result of dietary preferences as much as of regional origin. Information on muscle and organ lipids in green turtles is limited (Holland *et al.*, 1990).

Marine algae are clearly the principal basis of the diets of mid-Pacific green turtles (Balazs *et al.*, 1987) and any carbohydrate could be quickly broken down to acetate in the turtle's digestive tract (Bjorndal, 1980; Bjorndal *et al.*, 1991) and then resynthesized to 12:0 and 14:0. The lipid content of marine algae is very low and the types of polyunsaturated fatty acids variable (Ackman, 1981). There are usually numerous algal epiphytes as well as the main seaweed body. The absence of significant 18:2n-6 and 18:3n-3 in the depot fat of any of these turtles is evidence that, unlike the Atlantic coast situation, sea-grasses (actually terrestrial plants adjusted to a marine milieu and with photosynthetic lipids containing 18:2n-6 and 18:3n-3) are not involved. The C_{20} and C_{22} polyunsaturated fatty acids found in small amounts in Groups II and III could have come from floating Pacific seaweeds. In most marine algae 22:6n-3 is much less obvious than 20:5n-3 (Nichols *et al.*, 1985; Takagi *et al.*, 1985; Volkman *et al.*, 1989). In animals 5 and in four out of five cases in Group III this proportion is observed. Large green turtles thus biosynthesize most of their depot fats *de novo* from acetate and other volatile fatty acids (Bjorndal *et al.*, 1991) to suit specific biochemical needs relating to energy storage and to confer physical properties matching their body temperatures. The addition of the C_{20} and C_{22} polyunsaturated fatty acids seems to be purely adventitious and based on dietary factors. These fatty acids therefore offer opportunities for food chain research in marine turtles similar to those recently observed in the blue-banded sea-snake *Laticauda colubrina* (Ackman *et al.*, 1991).

Little is known about the functions of the fats of most reptiles (Derickson, 1976). Recent dietary and analytical studies with the American alligator (*Alligator mississippiensis*) provide parallels in the conversion of carbohydrate to body mass (Staton *et al.*, 1990a), and in deposition of the longer-chain polyunsaturated fatty acids (Peplow *et al.*, 1990; Staton *et al.*, 1990b). The depot fats from one study include 12:0 from a dietary source, coconut fat. This fatty acid was *not* deposited when not in the diet (Staton *et al.*, 1990b). Otherwise the depot fats responded as expected to dietary fatty acids and bioconversion of C_{18} polyunsaturated fatty acids to

Table 2. Distribution of saturated and monounsaturated acids in mole% in the triglyceride of leatherback turtle fat†

Glycerol position	Fatty acid					
	12:0	14:0	16:0	18:0	16:1	18:1
1	7	18	24	12	7	12
2	2	10	4	2	13	45
3	9	14	10	5	8	19

†From Brockerhoff *et al.* (1968).

C₂₀ and C₂₂ fatty acids did not lead to important deposition in depot fats.

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about 12 inches long, and all are mature by age ten, when they are about 15 inches long. A 12-inch female will have approximately 42,500 eggs, a 15-inch female 76,600 eggs, and an 18-inch female 266,000 eggs. Maximum adult size is 22 inches.



Brown rockfish, *Sebastes auriculatus*.

BROWN ROCKFISH

History of the Fishery

There is no regular monitoring of commercial landings of brown rockfish (*Sebastes auriculatus*); however, occasional large catches of brown rockfish do occur. In the San Francisco Bay area, freshly caught whole fish are in demand for sale in oriental restaurants.

The brown rockfish recreational catch from 1979 to 1986 averaged 296,000 pounds, or two to four percent of the total recreational rockfish catch in California. Northern and southern California catches are almost equal. In the Puget Sound area, brown rockfish are a major portion of the recreational catch.

Status of Biological Knowledge

Brown rockfish, sometimes called bolina rockfish, range from southeastern Alaska to central Baja California. They are widely distributed in shallow waters and bays, but have been taken to depths of 420 feet. Subadults are strongly residential to their home sites and often occur near piers and rocky points.

Both male and female brown rockfish begin maturing at about three years old, at which time they are around 10 inches long. Half of these are mature at five years old, when they are

Brown rockfish, as do all rockfish, bear their young live. Females release larvae into the pelagic environment during December and January, and may do so again during May and June. The larvae remain in the pelagic environment until they transform into juveniles, after which they enter benthic habitats near shore. Benthic juveniles are known to inhabit shallow water habitats, often in bays, and to migrate to deeper waters as they grow older.

Brown rockfish feed on progressively larger prey as they grow. During their early benthic stage, juveniles feed on small crustaceans, amphipods, and copepods, but when they grow to around 5 inches, shift to crabs and small fish. Adult brown rockfish (greater than 12 inches) feed on larger fish, shrimps, and crabs.

Little is known about predation on brown rockfish, but probably it is similar to predation on other rockfish species. Presumably, they experience the most predation during their pelagic larval and juvenile stages, and less predation as they grow larger. Probably adults are only occasionally taken as prey.

Status of Population

Without regular monitoring of catch data, there is no way to assess the brown rockfish population size. Currently, there are no indications of stress on these populations.

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COPPER ROCKFISH

History of the Fishery

Copper rockfish (*Sebastes caurinus*) occur only sporadically in California commercial catch records. Commercial landings of copper rockfish are small and often included in the category of "other rockfish"; however, three-month landings of over 14,000 pounds have been recorded from Eureka. Although currently there are no significant commercial landings of copper rockfish in the United States, they were reported as the most commonly caught fish in otter trawls in Puget Sound in the 1930's.

Copper rockfish are a small, consistent portion of the statewide recreation catch of rockfish, averaging from two to three percent. The catch has no apparent trend and ranges from a high of over 500,000 fish in 1980 to 238,000 fish in 1986. Approximately two-thirds of the California recreational caught copper rockfish are taken from Monterey south versus one-third from north of Monterey. Copper rockfish are a major component of the recreational fishery further north, particularly in the Puget Sound-British Columbia area.



Copper rockfish, *Sebastes caurinus*.

Status of Biological Knowledge

The copper rockfish and the whitebelly rockfish (*S. vexillaris*) are virtually identical in appearance, except that the whitebelly rockfish tends to be more reddish. The meristics of the two species are the same, but there are chromosomal differences. Both are shallow water species usually found in rocky areas, but may be found as deep as 600 feet. Very limited tagging indicates that adult copper rockfish are strongly residential. The copper rockfish ranges from the Kenai Peninsula, Gulf of Alaska, to Monterey, and the whitebelly rockfish from Crescent City to San Benito Islands, Baja California.

Male copper rockfish begin maturing at three years old when they are about 12 inches; one-half are mature at four years old or 13 inches; and all are mature by seven years old or 16

inches. Females begin maturing at five years old or about 12 inches; one-half are mature at six years old or 13 inches; and all are mature by eight years old or 16 inches. A 13-inch female will have approximately 97,000 eggs, a 16-inch female 245,000 eggs, and a 20-inch female 654,000 eggs. The oldest copper rockfish found to date is 35 years old and is from Canadian waters.

In California, larvae are released from the female in February, but, in Washington and British Columbia, they are released in March and April. These fish remain as pelagic larvae and juveniles in offshore waters until May. From late May until July, juvenile copper rockfish first appear in kelp habitats high up in the water column, and later migrate to the bottom. As they grow, copper rockfish move into more typical adult rocky reef habitats.

Adult copper rockfish feed primarily on crabs and fish. Studies in Humboldt Bay found juvenile Dungeness crab to be a major part of their diet. Copper rockfish feed on small fish such as herring, anchovies, blennies, and small surfperch, but also on occasion have eaten spiny dogfish. Juvenile copper rockfish feed on calanoid copepods, caridean shrimp, and gammarid amphipods.

Like other rockfish, coppers are most vulnerable to predation as larvae and juveniles. During these stages, they are prey to salmon, lingcod, other rockfish, marine mammals and birds. As they grow older and larger, they are susceptible only to occasional predation by lingcod or marine mammals.

Status of Population

Although there are no population or mortality estimates for copper rockfish, there is no indication that stocks of this species are overfished in California waters. In the Gulf of Alaska and British Columbia, copper rockfish are the target of an expanding hook and line commercial fishery, and this fishery is having a significant impact on those stocks. If such a fishery were to develop in California waters, this species would require monitoring.

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CANARY ROCKFISH

History of the Fishery

The commercial trawl catch of canary rockfish (*Sebastes pinniger*) in California has declined from over two million pounds to 183 thousand pounds in the nine-year period from 1981 to 1989. (Previous to 1981, rockfish landings were not recorded separately by species.) Eureka and Fort Bragg together contribute 88 percent of the canary rockfish trawl catch, which is only seven percent of the rockfish landings for Eureka, and eight percent for Fort Bragg. The only non-trawl commercial landings are in a small hook-and-line fishery that operates from San Francisco southward.

Canary rockfish represent a small but consistent portion of the sport catch. From 1979 to 1986, the average annual catch was 280,000 fish per year, slightly less than three percent of the total for all rockfish species. The average catch from Monterey northward was more than twice what it was to the south: 194,000 fish per year (five percent of the rockfish catch) as compared to 86,000 fish per year (one percent of the rockfish catch).



Canary rockfish, *Sebastes pinniger*.

Status of Biological Knowledge

Canary rockfish, referred to as orange rockfish in older reports, occur from Baja California to southeast Alaska. Their center of distribution is the Washington-British Columbia area, and in California they have commercial importance only as far south as Bodega Bay. Electrophoretic differences indicate that canary rockfish may have two separate subpopulations: one north, the other south of central Oregon. Canary rockfish have been caught at depths below 1,000 feet, but are taken in abundance only to 500 feet.

Canary rockfish grow rapidly until they reach maturity at about 16 inches, then more slowly to a maximum age of 60 years. Most populations have few individuals older than 20 years. For example, at one year, females average 6.7 inches and males 7.9 inches; at 4 years, females are 13.4 inches and males 13.8 inches; by age 12, females average 20.4 inches and males 19.7 inches. By age fifty they have added little length (females = 22.4 inches; males 21.2 inches.)

Females begin to mature sexually at 10.6 inches, reaching 50 percent maturity at 17.3 inches, and 100 percent maturity at 21.2 inches. Males begin to mature at 11 inches, reaching 50 percent maturity at 15.7 inches, and 100 percent maturity at

17.7 inches. A 10.6-inch female carries about 69,000 eggs; a 17.3-inch female about 489,000 eggs; and a 21.2-inch female about 1,113,000 eggs.

Canary rockfish are viviparous, meaning that the females bear free-living young and contribute some energy to their young while they are inside the mother. Males fertilize the females around December, and the females hold their young until December to March. Pelagic juveniles occur in the upper 100 feet of the surface waters from April to June. It is assumed that the juveniles descend to benthic habitats after mid-June.

Adult canary rockfish feed primarily on euphausiids. Next in importance as prey are fish: mainly myctophids and adult shortbelly rockfish which are most abundant in fall and winter diet. Gelatinous zooplankton and associated hyperiid amphipods are common prey, but are a minor part of the diet. Pelagic juvenile canary rockfish feed on copepods, and euphausiid eggs and larvae.

Predation on canary rockfish is most severe during the pelagic larval and juvenile stages. Juveniles (one to three inches) are commonly found in the stomach contents of chinook salmon. Undoubtedly other predators of juvenile fish (other fishes, mammals and birds, including the common murre) prey on juvenile canary rockfish. After the juveniles descend to the benthos and become adults, they are much less vulnerable to predators.

Status of Population

The canary rockfish catch has declined sharply during the last ten years, particularly in Eureka. The mean length of canary rockfish has declined approximately 10 percent during this period at both Eureka and Fort Bragg. While estimates of population size or exploitation rates for canary rockfish in California waters are unavailable, these declines warrant increased surveillance of this species.

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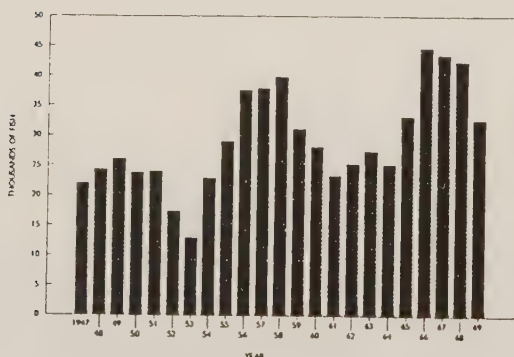
LINGCOD

History of the Fishery

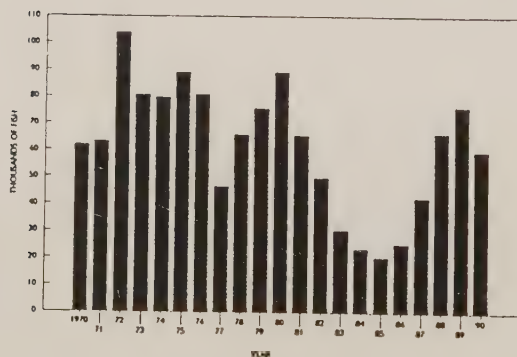
The lingcod (*Ophiodon elongatus*) is one of the largest northern California sport fishes. It is an aggressive predator that readily takes either a baited hook or an artificial lure, and it is a prized food fish. Although the raw flesh sometimes has a blue or green color, the flesh when cooked is white and of a mild flavor. From 1981 to 1986, lingcod provided more pounds of fish to

central and northern California recreational fishermen than any other species, including salmon. Only the rockfish group provides more pounds of fish to northern California recreational fishermen.

Annual landings averaged 51,250 lingcod from 1957 to 1961. At an average weight of eight pounds each, the annual yield was 410,000 pounds. The recreational fishery produced 20 to 25 percent by weight of all lingcod landed in those years. Twenty years later recreational fishermen were landing five times as many lingcod, but they were 20 percent smaller. From 1980 through 1986, annual landings averaged 254,000 fish per year. These fish averaged 6.2 pounds each yielding 1,575,000 pounds per year. The recreational fishermen's share has increased from a quarter to half of all lingcod landings.



California commercial passenger fishing vessel landings of lingcod, 1947-1969.



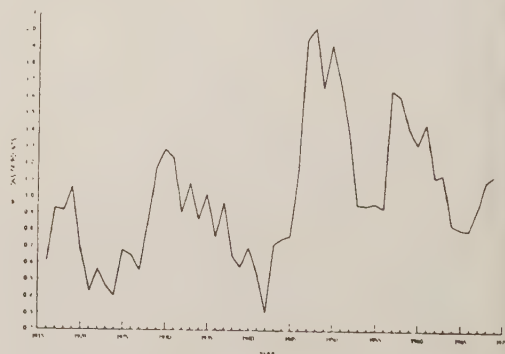
California commercial passenger-carrying fishing vessel landings of lingcod, 1970-1990.

Lingcod are most abundant north of Santa Barbara county, with eighty to ninety percent of the recreational landings being made north of San Luis Obispo County. Divers and recreational anglers both take lingcod. Divers use spears, and anglers use several styles of hook-and-line gear from a variety of fishing platforms. They may use either live or dead bait or artificial lures. Anchovies, squid, sanddabs, small rockfishes, kelp greenlings, and white croakers are used as live bait, while squid

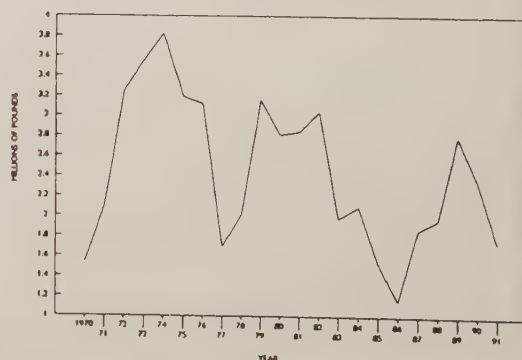
is the most common dead bait. Chrome plated jigs are the most popular artificial lures.

Recreational anglers catch lingcod while fishing from commercial passenger fishing vessels (CPFVs), privately owned boats (skiffs), piers, and the shore. In the late 1950's, 61 percent of the lingcod caught by recreational anglers were taken aboard CPFVs. However, the CPFV share of the landings declined to 33 percent in the early 1980's. Skiffs picked up the difference, increasing their share of lingcod landings from 32 to 58 percent. Shore and pier anglers and divers take a relatively small portion of lingcod landings; there appears to have been little change in their share.

Several steps have been taken to halt the decline in size of lingcod available to anglers. A 22-inch size limit was established in 1981, and the bag limit was reduced from ten to five fish one year later. These measures have slowed the decline but have not stopped it entirely.



California commercial landings of lingcod, 1916-1969.



California commercial landings of lingcod, 1970-1991.

The lingcod is also a valuable species in the fresh-fish market trade and is caught primarily north of Santa Barbara. It is frequently sold whole when landed in small quantities. A large lingcod makes an impressive addition to a display of fresh fish on a bed of ice. Hook-and-line caught lingcod are preferred for these displays, and fishermen receive a premium price for such fish because the fish's skin is not marred when they are

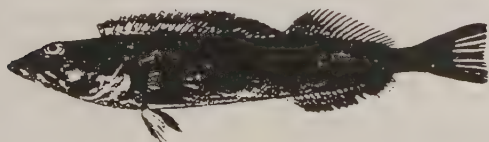
caught. Large catches of lingcod are usually filleted. Boneless portions can be cut from large fillets, and the flesh is slow to develop strong odors. These qualities contribute to the lingcod's commercial value. Commercial fishermen received \$1,020,000 for the lingcod they sold in 1989.

Recorded commercial landings in California have ranged from a low of 400,000 pounds in 1924 to a high of 3.8 million pounds in 1974. Larger quantities are taken off Oregon, Washington, British Columbia, and Alaska. Most of the landings preceding World War II were caught by hook-and-line fishermen. Before 1946, commercial landings fluctuated between 1,288,000 pounds in 1930 and 314,000 pounds in 1942, averaging 758,000 pounds per year.

With the introduction of the balloon trawl during World War II, trawl gear became the most important source of lingcod landings. Landings increased to 2,056,000 pounds in 1948, and then declined to 800,000 pounds in 1966. Landings began to recover in the late 1960's, and climbed sharply in the early 1970's reaching a new high of 3,824,000 pounds in 1974. This increase in landings during the 1970's had at least two causes. Lingcod experienced exceptional reproductive success during the late 1960's, and gill nets became an important means of catching rockfish and lingcod at Monterey. Since 1970, a large portion of the commercial lingcod catches south of San Francisco have been taken in gill nets.

During the 1980's, two-thirds of the commercial lingcod landings were taken by trawlers. Eighteen percent were taken with unknown gear and at least 13 percent were taken with gill nets. On average only 2.7 percent of the lingcod sold in the 1980's were caught on hook and line. However, as salmon populations declined and gillnetting was restricted, many fishermen converted to fishing for rockfish and lingcod with hook and line. Hook-and-line landings of lingcod increased seven fold from 1985 to 1989, producing 30 percent of the commercial lingcod landings in 1989.

Trawling is generally prohibited within three miles of shore. Most of the adult males and many of the adult females and juveniles feed in these nearshore areas. Gillnetting for rockfish has recently been prohibited in state waters, further protecting both juvenile and adult lingcod.



Lingcod, *Ophiodon elongatus*.

Status of Biological Knowledge

Lingcod are found only off the west coast of North America. They are distributed in nearshore waters from northern Baja California to the Shumagin Islands along the Alaska Peninsula. Their center of abundance is off British Columbia, and they become less common toward the southern end of their range. Lingcod are found over a wide range of substrates at

depths from 10 to 1,300 feet, but most occur in rocky areas from 30 to 330 feet.

Adult lingcod are strongly residential, tending to remain near the reefs or rocky area where they live. Large-scale tagging studies in Canadian waters have found that the vast majority of mature lingcod are recaptured within six miles of where they were tagged. Individual fish do make long movements, however, and one fish that was tagged at Cordell Bank was recaptured nine months later at Coquille Bank, Oregon, over 430 miles away. Juveniles tend to disperse and travel over a wider range than adults.

Lingcod growth follows a typical pattern of rapid increases in length during the first years of life, followed by progressively smaller increases. Although there is large variation in length at age, the average one-year-old fish is 13 inches, and a two-year-old is 17 inches. After age two, females begin to grow faster than males. The average four-year-old female is 24 inches, an eight-year-old is 32 inches, and a 12-year-old is 35 inches. The average four-year-old male is 22 inches, an eight-year-old is 29 inches, and a 12-year-old is 32 inches. In California, the oldest lingcod on record is a 14-year-old, 37-inch female, while the longest is 43 inches. The maximum age recorded anywhere is 20 years, and a 59-inch British Columbia lingcod weighed 70 pounds.

Both sexes mature over a wide size range. In California, some females mature at 20 inches, half are mature at 23 inches, and all are mature by 28 inches. Some males mature at 14 inches, half are mature at 16 inches, and all are mature by 22 inches. Size at maturity is larger for lingcod in more northerly latitudes because these fish grow faster.

Lingcod have a unique form of reproduction which includes spawning migrations into nearshore habitats, reproductive territoriality by males, spawning of an egg mass to form the nest, and the presence of a guardian male at the nest until the eggs hatch. In California waters, spawning begins by November and continues until March, with a peak in December and January. Males move into the spawning grounds first to establish territories, and it appears that larger males select the most suitable nesting sites. Preferred nest sites are rocky areas in shallow water (low tide line to 100 feet) where there are strong currents. A relatively strong current is necessary to oxygenate the egg mass and prevent death of the embryos. Often, egg masses are located on rocky ledges with an opening directly behind the eggs to allow water to pass over the nest. Laboratory studies show that a current with a velocity of four to six inches per second is necessary to provide adequate oxygen levels throughout the egg mass.

Lingcod probably spawn at night. After a female chooses a male and a nesting site, she swims over the site and deposits a layer of several eggs. The male then swims over the site and fertilizes the eggs. This process is repeated until spawning is completed, after which the female immediately leaves the spawning grounds. The eggs become firmly cemented to each other within the gelatinous mass in 24 to 48 hours. A 24-inch female can produce 50,000 eggs, a 32-inch female 124,000 eggs, and a 36-inch female 170,000 eggs. Egg masses of three to 68 quarts have been reported.

After spawning, males remain to guard the nests from predation until hatching is complete. Males position them-

selves within three feet of the nest and drive away potential predators. On occasion, males have been found guarding two nests if they were close together. If the male is removed, a new male will sometimes assume the guardian role. Males have very aggressive behavior during nest guarding and, therefore, are particularly vulnerable to fishing at this time. An unguarded egg mass is invariably eaten by predators. The eggs generally hatch about seven weeks after they are laid, but incubation can last from five to 11 weeks. Eggs on the outside of the egg mass hatch first. Hatching may continue for 24 to 48 hours, after which the guardian male leaves.

Newly hatched larvae (0.25-0.5 inch) occur in January and February in Humboldt Bay and San Francisco Bay. In Canadian waters, the first appearance of these larvae is in early March. From March until June, lingcod grow about 0.04 inch per day, transforming into pelagic juveniles. Juvenile lingcod may be caught off central California from April (at two inches in length) to June (at three inches) in pelagic trawls in the upper 100 feet of the surface waters. After June, these juveniles disappear from surface waters and migrate to bottom habitats, frequently around kelp and eelgrass beds. Lingcod appear in typically adult habitats at about 12 inches.

Larval lingcod feed primarily on various life stages of copepods. During the pelagic juvenile stage, there is a gradual transition from a diet of small copepods to one of larger copepods, crab larvae, amphipods, euphausiids, and herring larvae. As small benthic juveniles, lingcod feed on herring, flatfishes, shiner perch, and other fishes. Even young lingcod have a very large mouth for their body size, allowing them to feed on prey much larger than other fish of their age and size.

For large juvenile and adult lingcod, fish is the dominant prey, accounting for about 80 percent (by volume) of the stomach contents. In California waters, juvenile rockfishes are the most important prey. When the stomachs of nest-guarding males are examined, they are invariably found to be empty.

Most predation on lingcod occurs during the egg stage, and predation becomes less common with age. The presence of a nest-guarding male prevents fish predators, often other greenlings and surfperches, from consuming the entire egg mass; when the guardian male is removed, the entire egg mass is lost. Invertebrate predators such as predatory snails commonly feed on egg masses and are not repulsed by guardian males. On rare occasions, pelagic juvenile lingcod (1.5 to 2.6 inches) are found in the stomachs of chinook salmon from the Gulf of the Farallones. It can be assumed that other predators of juvenile fish, such as seabirds, particularly the common murre, and marine mammals, prey on juvenile lingcod at a similar rate. Small benthic lingcod are not usual prey of nearshore predators. Because of their large size, large juvenile and adult lingcod escape all but the occasional predator.

Status of Population

Fishing success is currently our only long-term indicator of changes in the abundance of lingcod. Commercial and recreational landings exhibit regular fluctuations with a periodicity of about ten years; commercial landings having peaked seven times in the past 73 years.

Recreational fishing success has exhibited regular fluctuations over the past 40 years, with each peak falling within two years of a peak in commercial landings. Peak landings of lingcod have been preceded by reports of sightings of small lingcod. SCUBA divers occasionally see large numbers of small lingcod less than one year old. Sightings were reported three to five years before each of the last three peaks. The years of exceptional lingcod abundance are probably the result of especially good survival of lingcod larvae. Although divers saw some small lingcod in 1988 and 1990, they were much less abundant than the 1984 cohort that produced the peak sport and commercial landings of 1989.

The population is still strong and is still providing landings of a size similar to those made early in this century. There is no long term trend in commercial landings. There has, however, been a five-fold increase in recreational landings in the past two decades and a 20 percent decline in the average weight of recreationally-caught lingcod. The decline in average weight is accompanied by a considerable reduction in longevity of lingcod. This trend must be stopped to ensure the existence of a spawning biomass large enough to produce an abundance of larvae when oceanic conditions are conducive to their survival.

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First attempt to determine birthdates and environmental relationship of juvenile sardine, *Sardina pilchardus* (Walb.), in the region of Vigo (NW Spain) during 1988

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ABSTRACT

The birthdate of juvenile sardine, Sardina pilchardus, from the Vigo region was determined from the number of daily increments in the otoliths. The majority of the fish were born during the first part of May to early June, which corresponds to the beginning of a period of calm weather.

Key words: Sardine, juvenile, birthdate, weather conditions, Spain.

RESUMEN

Relación entre fechas de nacimiento de juveniles de sardina, *Sardina pilchardus* (Walb.), y parámetros medioambientales en la región de Vigo (NO de España) durante 1988. Primera aproximación.

Se ha determinado el día de nacimiento de juveniles de sardina Sardina pilchardus del área de Vigo a partir del número de incrementos diarios en los otolitos. La mayoría de juveniles han nacido en el periodo comprendido entre la primera parte de mayo y principios de junio, que corresponde al principio de un periodo de calma.

Palabras clave: Sardina, juveniles, nacimientos, medioambiente, España.

INTRODUCTION

Lack of scientific understanding of the mechanisms controlling recruitment variability is widely recognized as the key problem area in fishery science at the present time. Marine fishes are generally known for their high mortality in the early life stages, and this is considered one of the main factors affecting population size. This feature led to the critical period hypothesis (Hjort, 1914, 1926) and its later variants, such as the match-mismatch hypothesis (Cushing, 1981), stability hypothesis (Lasker, 1981), larval

transport hypothesis (Parrish, Nelson and Bakun, 1981) and retention hypothesis (Iles and Sinclair, 1982). Much of the recent research on the recruitment problem has been structured from these theories. On the other hand, the observation of microincrements in the otoliths of fishes (Pannella, 1971, 1974) and its daily nature (Brothers, Matthews and Lasker, 1976) have supposed a remarkable discovery in fisheries research.

The age and birthdate of fishes can be estimated with precision using this methodology. Reviews of the technique of microincrements have emphasized the neces-

sity of validation of the 1:1 nature of increments and age in days (Campana and Neilson, 1985; Jones, 1986). The daily nature of microincrements in the otoliths of *Sardina pilchardus* has been demonstrated by Ré (1984) from edge analysis. Birthdates of juvenile fishes were first calculated by Methot (1983), showing that these birthdates can be used to determine periods of high survival of pelagic fish spawn. Comparison of the survival index to short-term variability in environmental processes and conditions may reveal linkages and causal mechanisms.

It is the basic hypothesis of the Sardine Anchovy Recruitment Program (SARP) that the technique of daily microincrements can be used to investigate the process of recruitment in clupeoid fishes. In this paper, we present the first attempt to determine the birthdates of juvenile sardine off NW Spain and its possible relationship to environmental variables, such as calm weather.

MATERIAL AND METHODS

Only two samples of young sardine were obtained from the purse seine fishery in Vigo, on September 24 and 29, 1988. The total length of 95 and 96 individuals were measured, respectively (fig. 1, 2). The sagitta (hereafter otoliths) were removed, cleaned and mounted on microscope slides with Eukitt mounting medium. Otoliths from 25 randomly-selected fish from each sample were used. Total length of these 50 fishes ranged from 7.5-9.5 cm (fig. 3).

Daily microincrements in the otoliths were accurately read and recorded, using a compound microscope with 5, 16, 40 and 63 X objectives illuminated with polarized light. A closed circuit television camera was mounted on top of the microscope and the image was relayed to a video monitor. A digitizer with a precision of 0.13 μm interfaced with the monitor and a microcomputer (Methot, 1981). To reveal the inner microstructure, otoliths were ground with wet grit sandpaper.

A series of readings along the counting path running from the focus to the postrostral margin was made. Between successive readings, the otolith was polished to im-

prove the resolution and reveal more microincrements until the entire path was analyzed. Occasionally, the microstructure of daily increments was difficult to resolve within short (40-60 μm) segments of the otolith. In these cases, their number and width were interpolated by averaging the widths of the rings immediately preceding and following that segment, and dividing the mean into the segment length.

Usually such averaging involved only about 10% of the total microincrements observed. In most cases (70%), only one otolith was used, unless it was damaged or destroyed due to the destructive nature of the preparation method.

To interpolate the number of microincrements near the focus, we assumed that the width of the first microincrement was 1.5 μm and the distance from the focus to the first microincrement was 8 μm . We based this assumption on the average measurements of these parameters. To estimate the time between hatching and first feeding, we used embryonic growth rates determined in rearing conditions (Miranda, Cal and Iglesias, 1990) and the temperatures recorded at three stations off the Ría de Vigo during the month of May. These temperatures ranged from 14.7 to 16.5°C (mean 15.3°C). At 15°C, sardine eggs hatch in 4 days and the eyes become pigmented 8 days after fertilization. Thus, 4 days were added to the number of daily microincrements in the otoliths to calculate the day of hatching.

Data on environmental conditions were estimated from geostrophic winds in a station located in front of the Ría de Vigo at 42° N. The data set is made up of 6 hourly observations and contains a north-south component and an east-west component (Smith and Bakun, 1989).

RESULTS

The birthdates or day of hatching of the 50 fish studied ranged from 130 to 160 Julian days of 1988, corresponding to May 10 to June 9. The mean birthdate was May 25. These birthdates corresponded to the beginning of a period of calm weather (fig. 4).

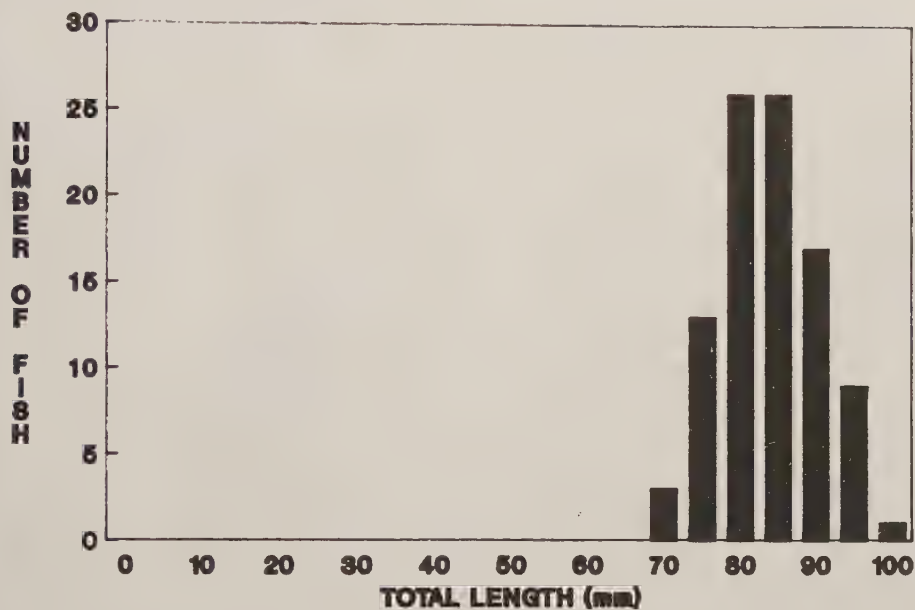


Fig. 1.—Size distribution of sardine juveniles sampled on September 24, 1988 (n = 95).

Fig. 1.—Distribución de tallas de juveniles de sardina muestreados el 24 de septiembre de 1988 (n = 95).

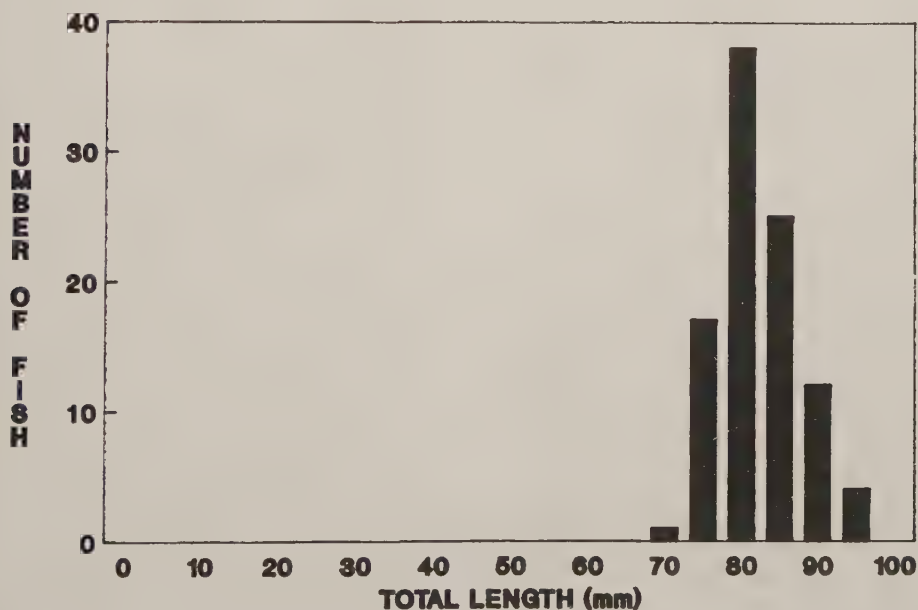


Fig. 2.—Size distribution of sardine juveniles sampled on September 29, 1988 (n = 96).

Fig. 2.—Distribución de tallas de juveniles de sardina muestreados el 29 de septiembre de 1988 (n = 96).

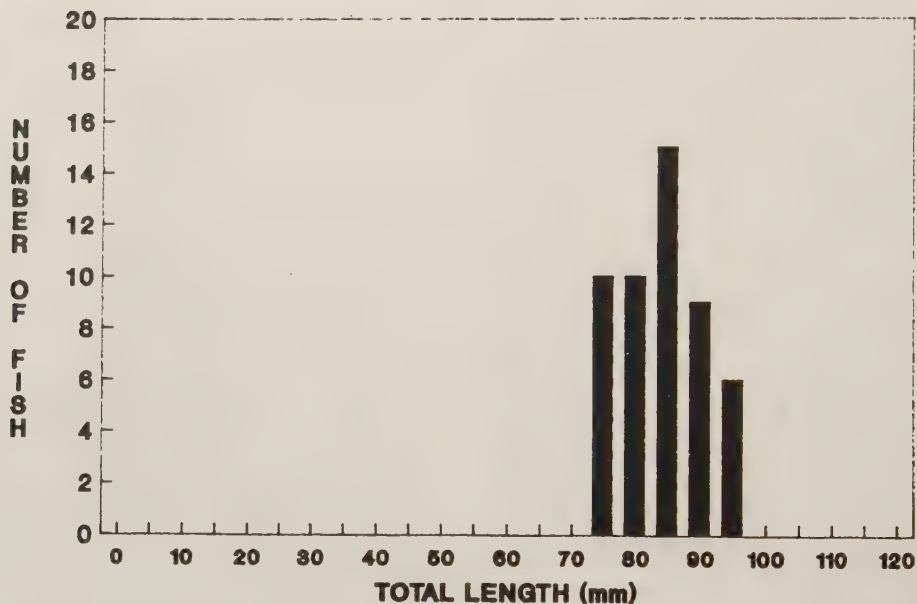


Fig. 3.—Size distribution of sardine juveniles for which age was determined ($n = 50$).

Fig. 3.—Distribución de tallas de juveniles de sardina a los que se determinó la edad ($n = 50$).

Sardina pilchardus — VIGO

Birthdates and Windspeeds 1988

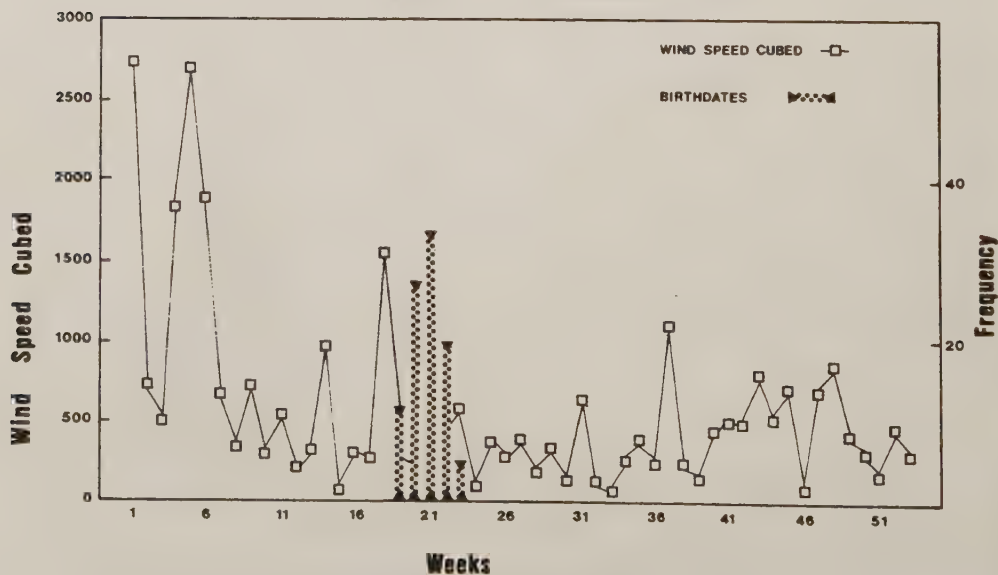


Fig. 4.—Birthdate distribution from 50 juveniles of the 1988 cohort off Vigo, compared to wind speed cubed from the same year. Wind data from Smith and Bakun (in press).

Fig. 4.—Comparación entre las fechas de nacimiento de 50 juveniles de la cohorte de 1988 en la región de Vigo y el cubo de la velocidad del viento del mismo año. Datos del viento de Smith y Bakun (en prensa).

DISCUSSION AND CONCLUSIONS

Recruitment variability in the sardine stock of the Atlantic Iberian Peninsula has been quantified during the past decade (Porteiro, Álvarez and Pérez, 1988; Anon, 1990). Recruitment was poor in 1988. Sampling difficulties arose due to low juvenile catches by the purse seine fleet based in Vigo port.

Sardine presents a protracted spawning season, from early autumn to the end of spring (Andreu, 1955; Ferreiro and Labarta, 1982; Pérez, Porteiro and Álvarez, 1985).

A recent work based on ichthyoplankton samples collected on a monthly basis at three locations off the N-NW Iberian Peninsula from 1987-1989 pointed out that spawning can last practically all year round, with the main spawning period in spring (April-May) (Solá *et al.*, 1990).

On the other hand, studies by Hunter and Goldberg (1980) and Hunter and Leong (1981) changed concepts about the reproductive biology of batch or multiple-spawning fish, and gave rise to a large number of studies on the reproductive biology of small, schooling, batch-spawning clupeiform fish in different ecosystems (Alheit, 1991). These aspects were investigated in the Iberian Atlantic sardine, and estimations of relative batch fecundity, spawning frequency and daily specific fecundity were obtained (Pérez *et al.*, 1989; García *et al.*, 1991).

This spawning strategy could be interpreted as an adaptation to an unpredictable environment such as the upwelling system, which is well known in the Atlantic waters of the Iberian Peninsula (Wooster, Bakun and McLain, 1976; Fraga, 1981; Cabanas *et al.*, 1988). To ensure that at least some of the eggs and larvae survive to be recruited, mature fish spawn intermittently in batches over a protracted spawning season, improving the chances that at least some eggs or larvae are present when an unpredictable "survival window" is opened (Peterman and Bradford, 1987; Curry and Roy, 1989). Our data would indicate that the birthdates correspond to the beginning of a period of calm weather, and they are consistent with the Lasker hypothesis (1981) that first-feeding larvae require adequate food supplies for growth and survival. In a later work on

the possible causes of variability in this stock, based on the monthly capture of juveniles in southern Galicia ports and their birthdates and environmental parameters (Robles, Porteiro and Cabanas, 1991), some links between recruitment anomalies and those parameters have been identified. So, variations in recruitment can be explained on the basis of fluctuations in "environmental windows" during the periods of spawning and larval drift. Weak upwelling and abundant food would determine the success of spawning. Our results should also be in accordance with this conclusion.

However, it should be pointed out that Robles, Porteiro and Cabanas (1991) have carried out a qualitative attempt to explain the relationships studied, and our results are based on a very limited number of samples.

Smaller, and hence younger, recruits may not be represented in these samples. Thus, recruits from the calm period lasting into July may not be represented. To carry out a complete test of the hypothesis under study in SARP, birthdates distribution of unbiased samples of the survivors of the larval stage, the recruits, should be compared with the seasonal distribution of spawning, determined from ichthyoplankton surveys conducted throughout the spawning season over the entire habitat at short intervals. The reason is that larval production can vary on small space scales as well as on small temporal scales. Because of the extensive ship time and other operational resources required, no fully elaborated SARP "within year" exercise, incorporating a full suite of environmental and biological aspects, has been completed to date. Nevertheless, the EUROSARP cooperative project will be implemented in the period 1990-1992 with EEC funds. The project concentrates on North Sea spratt (*Sprattus sprattus*), sardine off the Iberian peninsula and anchovy (*Engraulis encrasicolus*) in Portuguese estuaries. The project includes the "high temporal resolution" exercise as well "high spatial resolution" studies (Bakun, Alheit and Kulenberg, 1991), and is expected to provide very valuable insights into the recruitment processes of clupeoid fishes.

ACKNOWLEDGEMENTS

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MARINE BIRD RESOURCES

Seabirds are a diverse assortment of bird species that inhabit salt or brackish water environments for at least a part of their annual cycle. This discussion is limited to the pelagic species of birds that breed on offshore islands and make their living by utilizing the food web in the upper layers of the ocean in contrast to the waterfowl (ducks, geese, grebes, loons,

wading birds, and shorebirds) that live mostly in the coastal marsh areas or nest in arctic tundra or inland lakes and marshes. Seabirds can be further divided into resident (breeding) and non-resident (not breeding) species. Birds in these ecological categories are very different in how they affect or are affected by the natural environment and human-related events along our coast.

Table 1. Seabirds which breed off the California coast, their distributional status relative to areas north and south of California, the approximate sizes of their breeding populations in the 1980's and their status in the 1990's (X indicates presence, 0 indicates absence).

Common Name (Scientific Name)	Distribution in:			Estimated CA Breeding Pop. in the 1980's ²	CA Status in the 1990's
	Alaska	California ¹	Baja Cfa		
Forked-tailed storm-petrel (<i>Oceanodroma furcata</i>)	X	X	0	300	Unknown
Leach's storm-petrel (<i>Oceanodroma leucorhoa</i>)	X	X	X	18,300	Declining
Ashy storm-petrel (<i>Oceanodroma homochroa</i>)	0	X	0	5,200	Unknown
Black storm-petrel (<i>Oceanodroma melania</i>)	0	X	0	150	Unknown
Brown pelican (<i>Pelecanus occidentalis</i>)	0	X	X	2,700	Increasing
Double-crested cormorant (<i>Phalacrocorax auritus</i>)	X	X	X	1,900	Stable/Increasing
Brandt's cormorant (<i>Phalacrocorax penicillatus</i>)	0	X	X	64,200	Stable/Increasing
Pelagic cormorant (<i>Phalacrocorax pelagicus</i>)	X	X	0	15,900	Stable/Increasing
Western gull (<i>Larus occidentalis</i>)	0	X	0	51,000	Increasing
Common murre (<i>Uria aalge</i>)	X	X	0	363,200	Declining
Pigeon guillemot (<i>Cephus columba</i>)	X	X	0	14,700	Stable
Marbled murrelet (<i>Brachyramphus marmoratus</i>)	X	X	0	2,000	Declining
Xantus' murrelet (<i>Synthliboramphus hypoleucus</i>)	0	X	X	3,600	Stable/Declining
Cassin's auklet (<i>Ptychoramphus aleuticus</i>)	X	X	X	131,200	Unknown
Rhinoceros auklet (<i>Cerorhinca monocerata</i>)	X	X	0	400	Increasing
Tufted puffin (<i>Fratercula cirrhata</i>)	X	X	0	250	Stable
Number species in common		10	-	7	
Total breeding species	28 (30)	16 (23)	14 (22)		

¹Some species in Alaska or Baja California are not listed because they do not occur off California. The number of breeding species in California can be increased by adding up to five terns (*Sterna* sp.), the black skimmer (*Rynchops niger*), and the California gull (*Larus californicus*); numbers in parentheses indicate additions of this type for each area.

²The estimated Alaskan breeding seabird total population is about 40,200,000 compared to about 700,000 for California. These numbers represent approximate mean levels throughout the 1980's, and recent updates will be published in 1993. Ten to forty percent should be added to include non-breeders and immatures, a proportion which varies from year to year and species to species. In California four species (common murre, Brandt's cormorant, Cassin's auklet, and western gull) comprise almost 90 percent of the total number of breeders.

There are 23 species of seabirds that breed along the coast of California. Point Conception is generally considered a major area of transition between characteristically northern seabirds (such as those found in the Gulf of Alaska and Washington) and subtropical seabirds (such as those found in the Gulf of California). North of Point Conception, marine waters are dominated by the California Current System in which cold, nutrient-rich water is upwelled along the coast. South of Point Conception, upwelling mainly occurs only far offshore, and warmer, clearer, nutrient-poor waters extend up from the Subtropics. Ecologically, this makes California's marine birds among the most interesting and taxonomically diverse in the northern hemisphere.

California's breeding seabirds are about evenly divided between southern and northern species. The northern seabird species have a greater biomass, however. One of the reasons for this is that northern waters are generally more productive and, therefore, support greater seabird populations. In California, many of our breeding seabirds, such as common murre, Brandt's cormorants, and Cassin's auklets (all primarily northern species) are concentrated at the Farallon Islands (off San Francisco) and Castle Rock National Wildlife Refuge (near Crescent City). The Farallons are the most important single seabird breeding site in California, and large seabird populations there are associated with abundant availability of suitable and protected nesting habitat, coupled with strong and productive upwelling systems that provide large prey resources in the same area.



A brood of three California brown pelicans on Anacapa Island off southern California. Improvement in reproductive success is linked to a decline in DDE residues in the offshore environment.

Another major California breeding area south of Point Conception in the Southern California Bight is the Channel Islands. These islands harbor important nesting colonies for some seabirds of northern affinity (such as Cassin's auklets) but also the state's entire nesting population of brown pelicans (presently a recovering endangered species) and the rare Xantus' murrelet. Both species have southern breeding distributions and also nest off Baja California; but the brown pelican is of tropical affinity (origin), whereas the Xantus' murrelet is of subarctic affinity. One of the most unique and interesting breeding seabirds off central and northern California is the marbled murrelet, a small seabird that nests inland in coastal, old-growth coniferous forests, often over a hundred feet high in the tree tops. Unfortunately, this little bird is becoming endan-

gered because of the loss of its nesting habitat due to logging, and because of mortality caused by oil spills and gill-net fishing.

Usually, between the end of summer after the Upwelling Period and before the end of the year, the California Current System experiences an immigration, emigration, and reshuffling of seabirds from the north, south, and within California. The abundance and diversity of seabirds increases immensely at this time. One of the most abundant seabird species in the world, the sooty shearwater, comes through California waters by the millions, mostly from New Zealand. Another exciting sighting involves one of several species of albatrosses which seem to be showing up off California in increasing numbers. Similarly, southern seabirds, such as boobies, red-billed tropicbirds, and magnificent frigatebirds, can provide the highlight of any boat trip. From the Mexican Sea of Cortez around July, come several species of storm-petrels, Heermann's gulls, elegant terns, and many more brown pelicans than nest in California. From the north, especially into the winter, we witness the arrival of northern seabirds like the northern fulmar, tufted and horned puffins and other alcids, the black-legged kittiwake, the brant (one of the few species of wild geese that migrates along the coast to wintering areas in Mexico), and many others. Such diversity and abundance adds to the overall richness and value of California's total marine resources.

Table 2. Scientific names of birds mentioned in text but not included in Table 1.

Albatross	<i>Diomedea sp.</i>
Boobies	<i>Sula sp.</i>
Black-legged kittiwake	<i>Rissa tridactyla</i>
Brant	<i>Branta bernicla</i>
California least tern	<i>Sterna antillarum</i>
Elegant tern	<i>Thalasseus elegans</i>
Heermann's gull	<i>Larus heermanni</i>
Horned puffin	<i>Fratercula corniculata</i>
Magnificent frigatebird	<i>Fregata magnificens</i>
Northern fulmar	<i>Fulmarus glacialis</i>
Red-billed tropicbirds	<i>Phaethon aethereus</i>
Sooty shearwater	<i>Puffinus griseus</i>

History and Utilization

Marine birds or seabirds are the most conspicuous and familiar elements of marine communities, and are a source of pleasure and enjoyment for people at sea or along the coast. They are unique and important biotic elements of marine ecosystems and are good indicators of the general health of coastal offshore environments. Yet, people working or recreating at sea often know little about them. And, although often omitted from marine resource reference works such as this, seabirds require management and protection, just as do other elements of marine ecosystems.

Seabirds are prominent elements in the biodiversity of marine ecosystems. They perform what ecologist Paul Ehrlich calls "ecological services," such as nutrient cycling and scavenging of biological waste materials and debris from waters and

beaches. They often guide fishermen to fish. They are fun to watch, and consequently, contribute to local economies by attracting tourists. Healthy seabird populations give us the justified feeling that all is well at sea, and a "missing," sick, or oiled bird tells us that it might not be.

Like most marine wildlife, marine birds have historically suffered severe and relentless exploitations by man. In California, this was especially true at the Farallon Islands during and after the gold rush in the late-1800's, where common murrens were heavily exploited for their eggs. There was no regulation of take, and the murre populations incurred severe declines, so that only a few thousand individuals were left by the late-1920's. The Farallon murre population did not recover for several decades and even now is far below numbers of the 1800's. Exploitation of seabirds or seabird products is neither a local or recent phenomenon. Recall the ancient, managed harvest of guano by the Incas of Peru, or the harvest of guano for manufacturing gunpowder by the imperialistic navies of Europe in the 16th-18th centuries. Empires were won or lost over control of the seabird islands! Early sailors and explorers often utilized seabirds or their eggs, driving some species to the point of extinction. In general, however, there has been little success worldwide in utilizing seabirds for sustainable food or other product sources. The few exceptions include guano harvests in Iceland, harvest of cider down from seaducks in Iceland, "muttonbird" harvests (shearwaters) for oil in New Zealand, and the harvest of seabird guano from man-made islands off South Africa. There is no successful, sustainable harvest of seabirds or seabird products in California or the West Coast. Since the early days of exploitation, management has usually involved putting the nesting islands into a protection system. This is the case for most islands off California.

After World War II, California's abundant seabird populations began to suffer from new problems. For example, birds and marine mammals experienced population depletions as a result of offshore chemical pollutant discharges from industries in Southern California. In a different kind of example, bird populations in central and southern California declined from excessive sardine fishing. Many species of seabirds feed almost exclusively on surface-feeding fishes which are also sought in commercial fisheries. The depletion of sardines off Monterey is thought to have had deleterious effects on some species of seabirds. It is not well known, however, how long it takes to bring about a population decline of seabirds and how effectively various kinds of marine birds can switch to other prey. Since the 1950's, large oil spills and chronic waste oil discharges have become increasingly frequent, and large numbers of seabirds have been killed. Although acute oiling of seabirds (oil spills and the associated publicity they get) receives more attention, it might be that chronic oiling of the offshore environment causes the greatest damage to seabirds and other marine wildlife. Rehabilitation of oiled birds and mammals has not been very successful. Most birds die before rehabilitation can be attempted and many birds that receive care die anyway. Prevention of oil spills and chronic oiling is still the best solution.

Since seabirds are visibly affected when people misuse marine resources, the well-being of our seabird populations

helps tell us about the health of our oceans. Potential effects on seabirds are often examined to help evaluate the overall projected effects on the marine environment of future development activities. Such activities include increased levels of offshore oil extraction and transport; mining of other ocean resources; development of alternate forms of energy; use of new fishing techniques; fish farming and fish ranching at sea; and new marine product development and exploitation. Increasing levels of marine debris, including fishing gear and seemingly edible items made of plastic and other materials present other hazards. Additionally, "eco-tourism," a rapidly growing industry, can lead to unregulated intrusion onto nesting islands that are important to seabird populations. There is already a history of disappearance of seabird colonies on islands visited too frequently by unsupervised tourists. Global warming, if it occurs, may have detrimental effects on seabirds.

Recognition of the importance of seabirds as indicators and of the effects that human activities can have on them has led to a surge of activity and interest in seabird conservation and management. In addition to many governmental agencies, there are five "seabird groups" around the world composed of interested professionals which have been organized to study and help conserve these important elements of marine wildlife. The Pacific Seabird Group focuses on our West Coast from California to Washington, plus Alaska, Hawaii, British Columbia, and Mexico. In California, state and federal governmental agencies, anglers and commercial fishermen, and marine bird conservationists are beginning to work together to help conserve and manage marine wildlife.

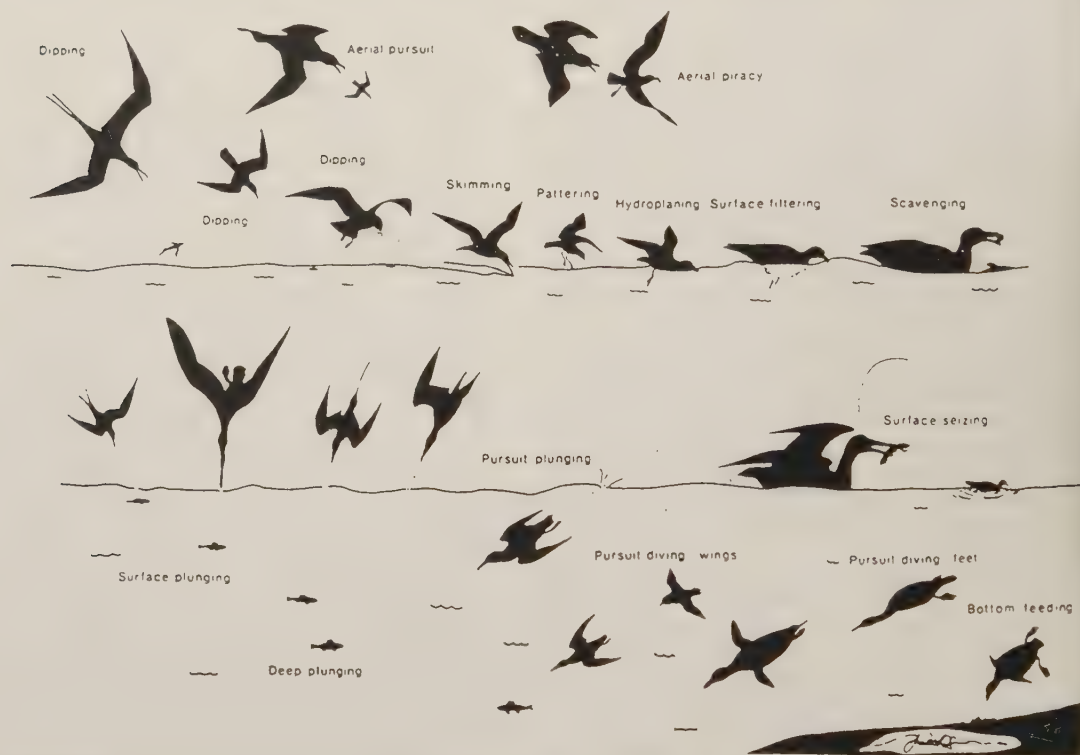
Seabird Ecology

Almost all important adaptations in body form and behavior of seabirds reflect specialization for either breeding or feeding. Methods of marine bird feeding depend on types of foods and where these foods are found in the water column. Seabirds are, therefore, influenced by the environmental factors which influence the marine environment. During the breeding season, seabirds are confined to feeding within a reasonable distance from their nesting islands. In addition to providing suitable nesting habit, nesting islands must be free of predators and disturbances. Outside the breeding season, when not constrained to tending offspring, many seabird species are highly mobile and can move long distances to find food. Other species may remain in areas of abundant and predictable food supplies, just like fishermen. Distribution at sea is heavily influenced by the physical oceanography of the area. For example, plankton feeders will be found where ocean currents favor growth and accumulation of planktonic species. Such areas, in turn, provide food for shoals of pelagic species such as northern anchovy, Pacific sardine, herring, mackerel, or juvenile demersal fishes such as rockfishes. These midwater fish in turn are preyed upon by fish-feeding seabirds. The species of fish is usually not as important as is the fact that the fish are available and abundant.

Some seabirds feed at the surface and others fly or paddle underwater to extend their reach lower into the water column. Some California species can dive to a depth of 330 feet. Water

clarity influences which type of feeding method will be most successful. For example, clear, tropical waters typically best support species that catch fish by plunge-diving (boobies and

pelicans). In contrast, northern waters are usually too turbid for aerial plungers to see prey, but are better suited to underwater swimmers or flyers (like the murres, auklets, and cormorants),



Seabird feeding methods in relation to depth of water column penetration and morphological variation of different species (described by N.P. Ashmole and drawn by J. Ahlquist, reprinted with permission from Academic Press).

While nesting, seabirds are more or less bound to a nest that requires protection from predators and parental care. The breeding season is the period of time it takes from courtship, nest-building, and egg-laying to the point of fledging, when young leave the nest or become independent. During breeding, seabirds are strongly influenced by local food supplies and, thus, the oceanographic and meteorological conditions. Reproductive success is influenced by the biomass, availability, and consistency of local food supplies. For instance, when El Niño weather patterns occur, seabirds reproduce poorly or not at all because prey resources are less abundant and available.

Since offshore islands with nearby, stable food supplies are in short supply for nesting seabirds in California, such birds are almost always found concentrated into tightly-packed nesting colonies, with different species usually segregated onto different kinds of micro-habitat. As a consequence, nesting colonies are vulnerable to destruction by mammalian predators such as foxes and raccoons. Therefore, nesting islands must be free from terrestrial predators and human disturbance to provide seabirds with successful nesting opportunities. Evolutionary development on islands lacking terrestrial predators has left

many seabirds with no defenses against predators, except to abandon their colonies. Undisturbed roosting and loafing sites are also critical to seabirds. Tourism and introductions of rats, cats, dogs, pigs, goats, and other feral animals has repeatedly led to extermination of seabirds from islands that were formerly predator-free.

Management

Many agencies are involved in the management and conservation of marine birds, and many statutory and executive provisions contribute to their protection. In addition, California has one of the finest systems of sanctuaries and refuges for seabirds in the world. However, our coastal wetlands now comprise only a small percentage of their former extent, and these habitats are critical to many species of seabirds. Offshore waters are becoming increasingly occupied and utilized by people, yet many offshore islands and rocks are as close to their natural states as one might reasonably expect in our modern world.

Nonetheless, some of California's seabirds are threatened or endangered, and others may warrant such designation. Examples are the California least tern, the California brown

pelican, the marbled murrelet, the Xantus' murrelet, and the ashly storm-petrel. The brown pelican may soon be downlisted because its populations are recovering; one of the few success stories in recent times.



Common murrelets and Brandt's cormorants on Flatiron Rock off Trinidad, north of Eureka.

Seabird populations have a number of characteristics in common which make them susceptible to harm from environmental changes:

- 1) Resident seabirds concentrate their nesting efforts over several months at small areas, and they traditionally use the same nesting areas year after year.

- 2) Some seabirds (pelicans, cormorants, gulls) concentrate in roosts or resting sites. Night roosts provide protection from predators and disturbances and may have beneficial thermal characteristics. Day roosts are located closer to food supplies and may have good plumage drying properties.

- 3) Many seabirds depend on concentrated food supplies, often commercially valuable fisheries resources. Marine fisheries biologists are working with marine wildlife biologists to balance recreational and commercial fisheries with other wildlife needs.

- 4) Many seabirds tend to be long-lived with low annual reproductive rates. Thus, seabirds cannot usually recover very rapidly from large impacts on their populations.

- 5) Seabirds are often components of assemblages with interdependent elements, which means that they are closely allied to other species in their system. Disruption of one or more interacting elements may affect the entire assemblage in some way.

Seabird and Fisheries Interactions

Seabird-fisheries interactions have been categorized as follows: 1) direct competition, with negative population implications either for fish or seabird populations; 2) mutualism,

where the interaction is beneficial, or commensalism, where there is neither benefit nor detriment to the interaction; and 3) physical injury, where birds are killed or damaged by fishing activities, or bird activities damage operations or gear. Categories 1) and 3) describe conflicts in resource use that should be minimized. Multi-species or ecosystem management instead of management that is single-species oriented may be the key to minimizing such conflicts. The management plan of the Pacific Fishery Management Council (PFMC) for anchovies was one of the first in the nation to consider the multiple uses of the anchovy resource, including seabirds, marine mammals, and bait fisheries for sport fishermen. With the rapidly recovering Pacific sardine resource, the PFMC is revising its anchovy plan to include multi-species management of small pelagic fishes. Fishery management plans are beginning to include concepts such as reserves, multiple-needs, ecosystem balance, and thresholds of minimum resource abundance.



Pileup of brown pelicans, Heermann's gulls, and Brandt's cormorants feeding on anchovies at Shell Beach. Other individuals are roosting on nearby rocks.

The future of fishing gear/seabird interactions is also improving. Gill netting has been banned in many areas, and some fishermen have switched to other fishing methods that do not harm seabirds. Situations are more difficult to control when the commercial fishing occurs outside areas of state or federal jurisdiction. Interactions between recreational fisheries and marine wildlife also occur. While each individual interaction may involve only one angler and one bird, together they can have a significant effect on some seabird populations, especially threatened or endangered species. In many instances the best management approach is education.

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Recovery metabolism of skipjack tuna (*Katsuwonus pelamis*) white muscle: rapid and parallel changes in lactate and phosphocreatine after exercise

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Lactate, glycogen, and high-energy phosphate levels were measured in serial biopsies from tuna white muscle during recovery from 15 min of enforced swimming. Exercise caused glycogen and phosphocreatine levels to decrease sharply and lactate concentration to increase markedly (up to $150 \mu\text{mol} \cdot \text{g}^{-1}$). Lactate was cleared from white muscle in less than 90 min, at rates comparable to those seen in mammals (about $1.3 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$), and this was accompanied by nearly stoichiometric increases in white muscle glycogen (2 lactate : 1 glucosyl unit). The plasma lactate concentration remained elevated (35–40 mM) until lactate clearance from white muscle was completed, whereas the level of plasma glucose was constant (12–16 mM) for the entire 3-h recovery period. The exercise routine caused minimal changes in white muscle purine nucleotides apart from a slight, but significant, increase in IMP content. Transient changes in ATP appear to have resulted from short-term intense swimming activity noted during anesthetization. Unlike other teleosts, lactate clearance in tuna paralleled creatine rephosphorylation during recovery from exercise. We suggest that the postexercise adjustment of intracellular pH is responsible for this relationship. Lactate was seemingly metabolized within the white muscle mass, as indicated by *in situ* conservation of lactate carbon apparent from stoichiometric increases in white muscle glycogen levels. This prospect is discussed in view of low estimates of lactate utilization rates by other tissues and contrasted with expected high rates of whole-body lactate turnover during recovery.

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Le lactate, le glycogène et les phosphates utilisés pendant l'effort ont été mesurés dans des biopsies en séries prélevées dans le muscle blanc de Thonines à ventre rayé au cours de la période de récupération consécutive à une nage forcée de 15 min. L'exercice a entraîné une chute brusque du glycogène et de la phosphocréatine et une augmentation marquée de la concentration de lactate (jusqu'à $150 \mu\text{mol} \cdot \text{g}^{-1}$). Le lactate est disparu du muscle blanc en moins de 90 min, à des taux comparables à ceux qui prévalent chez les mammifères (environ $1.3 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$) et sa disparition s'accompagnait d'augmentations presque stoechiométriques du glycogène dans le muscle blanc (2 lactates : 1 unité de glucosyl). Le lactate est resté présent en concentration élevée dans le plasma (35–40 mM) jusqu'à la fin de la clearance du lactate dans le muscle blanc, alors que le glucose plasmatique est resté constant (12–16 mM) durant toute la période de récupération de 3 h. L'exercice n'a causé que des modifications minimes des nucléotides de purine dans le muscle, à l'exception d'une augmentation légère, mais significative, du contenu en IMP. Des modifications temporaires du contenu en ATP semblent avoir résulté de la courte période d'activité de nage intense observée au moment de l'anesthésie. Contrairement à ce qui a été enregistré chez d'autres téléostéens, la clearance du lactate s'accompagnait d'une rephosphorylation parallèle de la créatine au cours de la récupération qui a suivi l'exercice. Nous croyons que l'ajustement du pH intracellulaire à la suite d'un exercice est responsable de cette relation. Le lactate semble être métabolisé dans la masse même du muscle blanc, puisque le carbone du lactate est conservé *in situ*, comme l'indiquent les augmentations stoechiométriques du glycogène dans le muscle blanc. Cette théorie est examinée à la lumière des valeurs peu élevées des taux d'utilisation du lactate dans les autres tissus et confrontée aux taux élevés de remplacement du lactate total auxquels on doit s'attendre au cours de la récupération.

[Traduit par la rédaction]

Introduction

Tuna can sustain relatively high speeds of 3–5 body lengths/s indefinitely, yet they are also capable of short-term speeds of up to 20 body lengths/s. This intriguing combination

of sprint and endurance abilities is supported by a metabolism with several unusual features. For example, skipjack tuna (*Katsuwonus pelamis*) are able to fuel burst swimming through an exceptional glycolytic capacity in white muscle, which can produce lactate concentrations of about $100 \mu\text{mol} \cdot \text{g}^{-1}$ (Guppy *et al.* 1979; Hulbert *et al.* 1979).

Removal of elevated plasma lactate and metabolically pro-

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duced protons following exhaustive exercise occurs very rapidly in tuna (Barrett and Connor 1964; Perry *et al.* 1985). In fact, rates of lactate turnover in postexercise tuna resemble those observed in mammals (Weber *et al.* 1986), suggesting that the circulatory translocation of lactate accounts for some portion of the white muscle lactate clearance in recovery. In contrast, other teleosts appear to retain most of the lactate formed during exhaustive exercise within the white muscle mass and require long periods for lactate clearance (Batty and Wardle 1979; Milligan and McDonald 1988).

The rate of recovery from exercise in muscle of tuna may also be more similar to that of mammals than to that of other teleosts. Barrett and Connor (1964) found that the glycogen content of tuna muscle recovers within, at most, 2 h following exercise, whereas recovery takes up to 12–24 h within trout muscle (Milligan and Wood 1986; Schulte *et al.* 1992). It is not known if the rate of recovery of other intracellular metabolites, such as lactate and phosphocreatine, is also rapid in recovering tuna muscle. In studies of recovery from exercise in other teleosts, such as trout, the fish is exercised and terminal samples are collected by freeze clamping at selected times after exercise. Muscular contractions during sampling can cause artefacts resulting from changes in the concentrations of intracellular metabolites such as phosphocreatine and ATP. Nevertheless, with care and rapid sampling, it has been possible to follow the changes in intracellular metabolites after exercise in trout (Pearson *et al.* 1990; Schulte *et al.* 1992). It is not feasible to use this approach for tuna since 'resting' skipjack typically swim at 1–2 body lengths/s to keep from sinking and to 'ram ventilate' the gills (Guppy *et al.* 1979). The capture of free swimming tuna is not compatible with the requirement to reliably collect tissue samples from tuna that have not struggled.

We have used an alternative method. Recently Bushnell *et al.* (1990) described a protocol for spinally blocking tuna, which permitted continuous measurement of cardiovascular parameters under controlled conditions. By using this procedure, and sampling muscle with a high-speed biopsy technique, we are able to separately collect and rapidly freeze muscle samples from the same fish at different times after exercise. The advantage of this approach is that we can analyze detailed muscle metabolite changes from individual fish and consequently use fewer fish overall to elucidate general patterns of recovery metabolism than would be necessary if using a terminal sampling procedure.

In the present study, the metabolism of white muscle carbohydrate and high-energy phosphate was investigated in tuna during recovery from exercise. The rate of lactate clearance from white muscle closely matched the rate of glycogen replenishment and, interestingly, paralleled the rapid rephosphorylation of creatine seen in exercise recovery. The rate of recovery is comparable to that seen in mammals, and we suggest that tuna conserve lactate to facilitate rapid recovery from exercise.

Materials and methods

Experimental animals

Live skipjack tuna, *Katsuwonus pelamis* (1–2 kg), were purchased from a local fisherman and maintained in outdoor holding tanks at the Kewalo Research Facility (Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration). The tanks were supplied continuously with aerated sea water at $25 \pm 2^\circ\text{C}$. Fish were not fed and were used for experiments within 3 days of capture.

Exercise and biopsy protocol

In preliminary studies, terminal muscle samples were taken to determine resting and postexercise levels of white muscle metabolites. Eleven unexercised fish were netted from the holding tank and killed with a sharp blow to the head. A sample of epaxial white muscle was dissected from behind the dorsal fin of each fish, freeze-clamped between Wollenberger tongs and immersed in liquid nitrogen as in earlier studies (Guppy *et al.* 1979). Very little struggling occurred during this procedure, and less than 20 s elapsed from the time of capture to the point of tissue immersion in liquid nitrogen. Three other fish were sampled in the same manner after first being isolated individually in another holding tank and chased with capture nets for 15 min. All dissected muscles were stored frozen over dry ice prior to homogenization and assay procedures. The two groups were designated unexercised freeze-clamped and exercised freeze-clamped, respectively.

A serial biopsy technique was developed to assess *in vivo* metabolite changes in tuna white muscle during recovery from exercise. Each fish was first exercised as described above, then captured by net and guided into a plastic bag containing buffered MS-222 (tricaine methane sulfonate, $1.0 \text{ g} \cdot \text{L}^{-1}$ with $1.0 \text{ g} \cdot \text{L}^{-1}$ NaHCO_3) dissolved in oxygen-saturated seawater. This group is referred to as exercised biopsied. Tuna taken from the holding tank and anesthetized without being chased served as unexercised controls and are referred to as unexercised biopsied. Immediately following anesthesia (about 2 min), each fish was placed on an operating table and the gills were irrigated with recirculated water containing a low level of anesthetic (MS-222, $0.1 \text{ g} \cdot \text{L}^{-1}$). At this time, initial biopsy samples were obtained from the epaxial muscle, using a 3-mm bore at 10–15 mm depth (ALKO Diagnostic Corporation). The tissue sample was drawn from the fish by suction into a chamber cooled with liquid nitrogen, and frozen almost instantly. Bleeding was minimal and was stopped easily by inserting a cotton applicator tip into the puncture. Skin was separated from the white muscle biopsy under liquid nitrogen and the sample stored over dry ice.

After the first sample was taken for biopsy, the fish was turned ventral side up on the operating table and the ventral aorta was cannulated following procedures described previously (Jones *et al.* 1986). The fish was then righted and a 20-gauge needle, 6 cm long, was inserted through the dorsal musculature (just lateral to the second spine of the dorsal fin) to the level of the spinal cord. Lidocaine hydrochloride (0.3 mL, 2% w/v) was then administered to establish a spinal block and arrest contractions of the swimming muscles. The needle was left in place for periodic re-injections throughout the experiment. Once secured in a foam-lined brace that was supported in a Perspex holding box (see Bushnell *et al.* 1990), the fish was presented with continuously flowing seawater ($35 \text{ L} \cdot \text{min}^{-1}$) and allowed to recover from anesthesia.

All subsequent samples for biopsy were taken from the tuna while in this restrained, spinally blocked position. To do this, the water level in the holding chamber was lowered to expose the back of the fish. The gills remained submerged during this time. Samples for biopsy were taken from an area directly lateral to the dorsal midline, 10–20 cm posterior to the spinal needle insertion site. Samples of white muscle and blood (0.25 mL) were taken at 20, 40, 60, 100, 120, 140, and 180 min into the recovery period. Plasma was extracted immediately from red cells by centrifugation, then deproteinized with one volume of 0.6 M perchloric acid and stored on dry ice. A terminal muscle sample was also taken after the fish was killed with a blow to the head at the end of the experiment.

Tissue preparation and analysis

Biopsy samples were homogenized with an Ultra-turrax tissue homogenizer in 2 mL of 8% perchloric acid in 40% ethanol that had been precooled over dry ice. Homogenization temperature was maintained below -20°C . A 50- μL aliquot of homogenate was removed for measurement of muscle glycogen, and the remainder was centrifuged for 10 min ($7500 \times g$, 2°C) in a Jouan table-top centrifuge. Potassium perchlorate was precipitated from the supernatant with 1 M KOH and the neutralized sample was stored on dry ice.

TABLE 1. Metabolites in white muscle of skipjack tuna

	Biopsies from spinally blocked tuna					
	Freeze-clamped unexercised (N = 11)	Initial		Final (180 min)		Freeze-clamped exercised (N = 3)
		Unexercised (N = 5)	Exercised (N = 4)	Unexercised (N = 5)	Exercised (N = 4)	
PCr (% total Cr)	74.6 ± 3.4	54.5 ± 9.6 ^a	20.1 ± 8.7 ^{a,b}	75.7 ± 3.2	76.5 ± 8.5	11.5 ± 4.7 ^{a,b}
Lactate (μmol · g ⁻¹)	7.3 ± 3.8	38.5 ± 10.4 ^a	107.5 ± 36.7 ^{a,b}	11.9 ± 8.1	14.9 ± 15.7	75.8 ± 4.8 ^{a,b}
Glycogen (μmol glucosyl units · g ⁻¹)	145.0 ± 34.4	127.3 ± 56.9	88.6 ± 32.4 ^c	145.6 ± 40.1	139.3 ± 53.6	74.6 ± 25.1 ^d
Pyruvate (μmol · g ⁻¹)	0.05 ± 0.01	0.39 ± 0.14 ^a	0.79 ± 0.30 ^a	0.05 ± 0.01	0.19 ± 0.09	0.14 ± 0.04 ^c

NOTE: Values are given as means ± SD. Freeze-clamped unexercised fish were taken directly from the holding tank, whereas freeze-clamped exercised fish were chased for 15 min and then killed immediately. Samples for biopsy were taken from both exercised and unexercised spinally blocked tuna. Differences were significant at $p < 0.05$.
^aSignificantly different from freeze-clamped controls and final biopsy (unexercised and exercised).
^bSignificantly different from initial biopsy, unexercised.
^c $p = 0.09$ for comparison with freeze-clamped controls, and $p < 0.05$ for comparison with final biopsy, exercised.
^dSignificantly different from freeze-clamped controls and final biopsy, unexercised.
^eSignificantly different from all means except final biopsy, exercised.

Total creatine (creatine (Cr) + phosphocreatine (PCr)) content remains constant for a given tissue (Connett 1988) and was used as an initial reference for all muscle metabolites measured. This is a reliable normalization procedure (Sabina *et al.* 1983) that avoids possible inaccuracies associated with weighing small, deep-frozen tissue samples. Conversion to micromoles per gram, for comparison with other studies, was made after determining total creatine content in tuna white muscle samples of known weight. A factor of 39 (μmol total creatine · g white muscle⁻¹) was used for these conversions.

Muscle lactate, glucose, Cr and PCr were measured according to Bergmeyer (1985), modified for use with microtitration plates (0.3 mL) and a Titertek Multiskan plate spectrophotometer. Pyruvate was determined fluorimetrically following Lowry and Passonneau (1972). Glycogen was measured in aliquots of white muscle homogenate and is presented as micromoles of glucosyl units per gram of tissue. Muscle glycogen was digested by incubating the homogenates for 3 h at 40°C with amyloglucosidase (Boehringer Mannheim, 2 mg · mL⁻¹) in acetate buffer, pH 4.8 (Bergmeyer 1985). Perchloric acid (25 μL, 70%) was used to halt the incubation, and glucose was determined in the extract after neutralization. Assays modified for the plate spectrophotometer were also used to measure glucose (Sigma Diagnostics assay) and lactate (Bergmeyer 1985) in the neutralized plasma samples.

The purine nucleotides adenosine triphosphate (ATP), adenosine diphosphate (ADP), adenosine monophosphate (AMP), and inosine monophosphate (IMP) were measured by high-performance liquid chromatography using an LKB 2152 controller and 2150 titanium pump coupled to a 2220 recording integrator. Column preparation and elution conditions were as described by Schulte *et al.* 1992. Briefly, an Aquapore AX-300 7-μm weak anion exchanger (Brownlee Labs) was used for the separation process, and detection was made using a BIO-RAD flow-through uv monitor (254 nm). An isocratic elution was established initially (60 mM KH₂PO₄, pH 3.2) for 5 min, followed by a linear gradient (60 mM KH₂PO₄, pH 3.2, to 750 mM KH₂PO₄, pH 3.5) over 10 min. The final concentration and pH were maintained for 12 min. Between runs the column was re-equilibrated for 6 min with the starting buffer. The column temperature was 55°C and the flow rate was 2 mL · min⁻¹ throughout.

Data analysis

Linear regression was used to determine break points in the curves describing the recovery of white muscle lactate and PCr. Break points were used as estimates of recovery time for these metabolites, and means from exercised and nonexercised tuna were compared using the two-sample *t*-test. Comparisons of all other metabolite concentra-

tions in the white muscle of the various groups of tuna were assessed with Tukey's multiple comparison test. Dependent *t*-tests were used to compare metabolite levels in biopsies taken at different times throughout the recovery period.

Results

Muscle metabolites after exercise

Terminal muscle samples from the exercised freeze-clamped tuna show significantly elevated lactate and pyruvate levels and depressed glycogen and PCr levels (Table 1), consistent with the utilization of anaerobic glycolysis to fuel intense white muscle activity. Similarly, the initial biopsy sample from the exercised biopsied fish had significantly elevated lactate and pyruvate and depleted PCr relative to that from the unexercised freeze-clamped tuna (Table 1). Glycogen in the first biopsy sample was reduced, but not significantly, compared with that in the unexercised freeze-clamped fish ($p = 0.09$), which likely reflects the large variation associated with these values.

An intermediate metabolite profile was observed in the initial biopsy samples of the unexercised biopsied tuna (Table 1), with lactate and PCr levels significantly different from those in both unexercised and exercised freeze-clamped fish. These changes were probably the consequence of the fish struggling prior to complete anesthesia, perhaps combined with a direct effect of the MS-222 anesthetic on muscle metabolism (see Van den Tillart *et al.* 1989).

It should be noted that the relative amount of Cr in the phosphorylated state is very high in tuna white muscle. In mammals and other teleosts, PCr levels of 30–50% of total creatine are typically measured. Van Waarde *et al.* (1990) suggested that, based on measurements with NMR, *in vivo* Cr was 80% phosphorylated in teleost white muscle, and they asserted that lower levels arise because of handling stress and (or) less than instantaneous freezing of tissue samples. The comparable values of 75% in white muscle of resting and recovered tuna presented in this study (Table 1) attest to the reliability of the freezing methods used.

There was a significant, yet transient, decline in ATP concentration in the exercised biopsied fish, but exercised freeze-

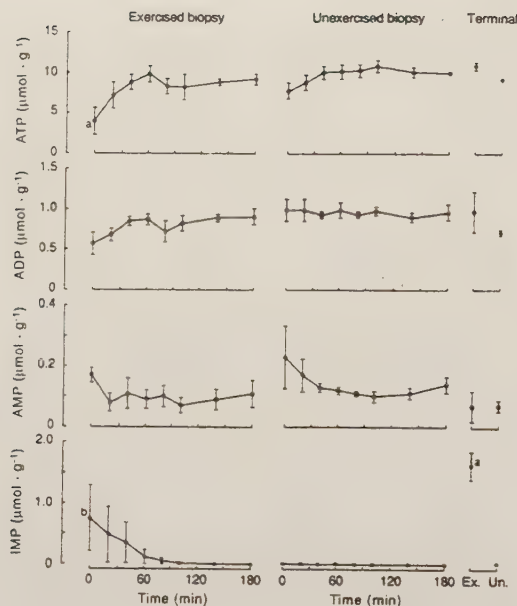


FIG. 1. Purine nucleotide levels (mean $\pm$ SE) in white muscle biopsies of unexercised ($N = 5$) and exercised ($N = 4$) tuna. Purine levels in muscle from terminally sampled, unexercised (Un., $N = 11$) and exercised (Ex., $N = 3$) fish are also shown. *a*, significantly different from Un., $p < 0.001$; *b*, significantly different from Un., $p < 0.05$.

clamped fish showed no changes in white muscle ATP relative to resting controls (Fig. 1). IMP increased significantly in both groups of exercised fish, whereas there were no changes evident in either of the ADP or AMP pools. No significant changes in the purine nucleotides were evident among the unexercised biopsied fish. Levels of white muscle purine nucleotides in all biopsied fish were indistinguishable from resting concentrations within 20–40 min after exercise.

Lactate, glucose, and glycogen in recovery

Changes in white muscle lactate and glycogen during 180 min of recovery from exercise are illustrated in Fig. 2. In both groups of biopsied fish the lactate recovery curves declined initially in a linear fashion and after 80–100 min remained constant at the pre-exercise level. Lactate concentrations in the final biopsy sample taken from exercised and unexercised biopsied fish were not significantly different from the resting level (Table 1). Biopsy glycogen concentrations were more variable than lactate concentrations in recovery, and significant differences between initial and final tissue levels were detected in only the exercised group (Table 1). However, most of the variation in recovering fish appeared to result from differences between individual fish. Consequently, *t*-tests on paired data indicate that glycogen concentrations in the white muscle of exercised biopsied fish were significantly higher in the final biopsy sample than at the start of the recovery period. Glycogen concentration in the final biopsy sample was not different from that of unexercised freeze-clamped fish at rest (Table 1) and, in fact, complete replenishment was evident at 80–100 min (glycogen concentration at 100 min was $154 \pm$

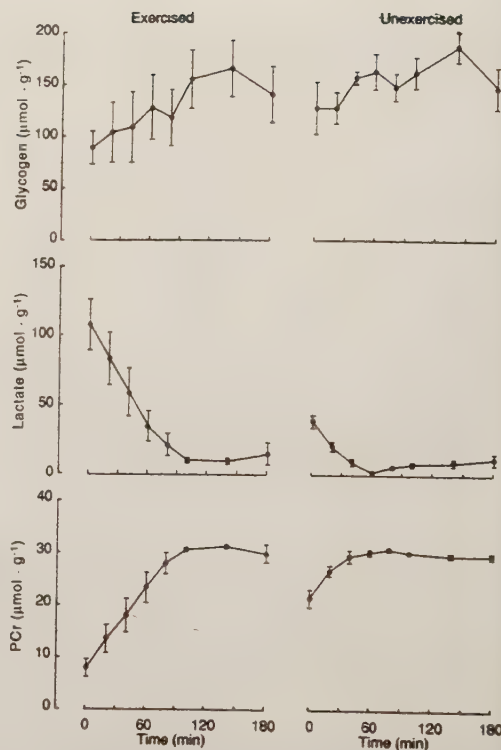


FIG. 2. Glycogen, lactate, and PCr levels (mean $\pm$ SE) in white muscle biopsy samples from exercised ($N = 4$) and unexercised ($N = 5$) skipjack tuna. See Table 1 for statistical analysis.

$55.5 \mu\text{mol} \cdot \text{g}^{-1}$, not significantly different from the final biopsy glycogen content).

The plasma lactate concentration in the exercised biopsied tuna was essentially steady, between 35–40 mM, during the first half of the recovery period (Fig. 3) and only began to decline after muscle lactate had reached the resting level. In the unexercised biopsied fish, plasma lactate content dropped steadily between 20 and 100 min recovery and remained constant thereafter at about 10 mM. Plasma was not obtained from unexercised freeze-clamped fish, but the apparent resting steady state achieved in recovery by the unexercised biopsied fish is comparable to previous measurements of plasma lactate in resting skipjack tuna (Perry *et al.* 1986).

The plasma concentration of glucose remained in a constant steady state throughout the recovery period in biopsied fish (Fig. 3). The glucose concentration averaged 12.9 ± 2.9 and 13.6 ± 3.5 mM (mean $\pm$ SD) for the control and exercised biopsied groups, respectively.

Estimates of recovery time (lactate and phosphocreatine)

Figure 4 depicts lactate and PCr concentrations in tuna white muscle from representative exercised and unexercised biopsied fish during recovery. Every fish showed the same general recovery pattern consisting of an initial phase of rapid change in lactate and PCr levels followed by a period in which the levels of these metabolites changed much more slowly. Both

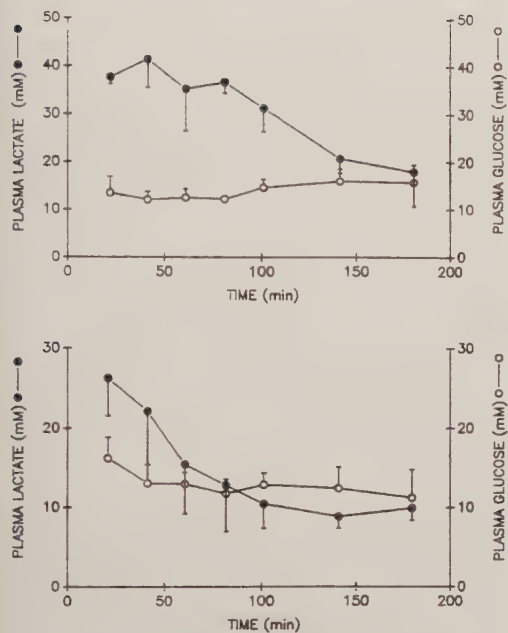


FIG. 3. Lactate and glucose levels (means $\pm$ SE) in plasma of spinally blocked tuna during recovery from exercise. Upper panel, fish that were exercised for 15 min. Lower panel, unexercised controls.

stages were linear, which permitted the estimation of recovery time by solving a set of regression equations for each of the fish biopsied. This analysis assumes a homogeneous distribution of muscle metabolites, which appears to be valid on the basis of the consistent changes in lactate and PCr levels observed during recovery for each fish despite random selection of biopsy sites. The variability in muscle glycogen content during recovery prevented the use of the breakpoint determination procedure on these data.

It became apparent that the experimental protocol produced a wide range of recovery times, rather than two discrete groupings, which reflected the degree of muscle lactate accumulation or PCr depletion. This essentially agrees with the earlier observation that the unexercised biopsied fish exhibited a muscle metabolite profile that was intermediate to that of the resting and exercised freeze-clamped tuna, probably resulting from the uncontrolled activity during anesthetization. The recovery times overlapped somewhat between exercised and unexercised biopsied fish, and therefore it seemed more appropriate to consider recovery time as a continuum with respect to exercise intensity. This is emphasized in Fig. 5, in which recovery time is displayed as a linear function of the concentration of both lactate and PCr in the first biopsy sample obtained from individual fish. As a result of this overlap, the average lactate (and PCr) recovery time for the exercised biopsied fish was only marginally different from the lactate (and PCr) recovery time for the unexercised biopsied fish (Table 2).

Another interesting outcome of the comparisons in Table 2 was that the time necessary for lactate recovery, for either the

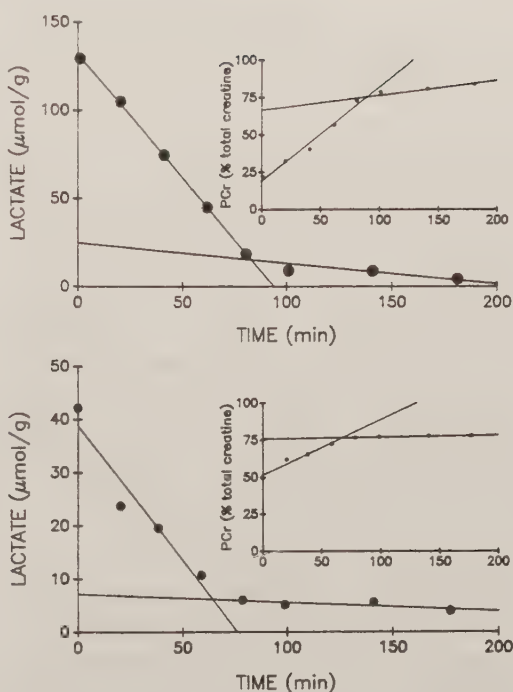


FIG. 4. Lactate and PCr in white muscle of representative spinally blocked tuna, showing regression lines for determining break points in metabolite recovery. Upper panel, a fish that was exercised for 15 min. Lower panel, an unexercised spinally blocked fish.

exercised or nonexercised biopsied fish, was not significantly different from the respective PCr recovery time. Furthermore, if individual biopsied fish were once again considered, then there was a striking synchrony between the rates of lactate disappearance and PCr repletion (Fig. 6 inset). There was also a close relationship between the concentrations of lactate and PCr in the individual biopsy samples (Fig. 6). This suggests that, unlike other teleosts that have been studied, some regulatory mechanism seemingly operates to tightly couple major adjustments of these metabolites in tuna white muscle.

Discussion

Muscle lactate and glycogen recovery

The disappearance of white muscle lactate levels at a rate of $1.3 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$ is up to 20 times faster than has been measured for trout ($0.055\text{--}0.12 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$). This unusually rapid clearance of lactate is intermediate between the rate of clearance for humans ($0.66 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$) and rats (about $2.5 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$) following maximal exercise (Hermansen and Vagge 1977; Meyer and Terjung 1979).

Weber *et al.* (1986) noted that despite high rates of whole-body lactate turnover in tuna, lactate recovery apparently occurs too quickly in white muscle to result from turnover alone, suggesting that some portion of the lactate remained in the white muscle as a substrate for postexercise, *in situ* metab-

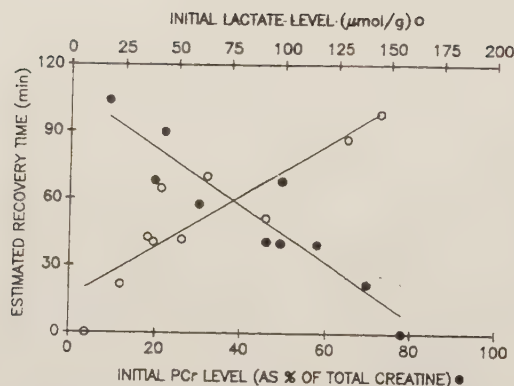


FIG. 5. Estimated recovery time in relation to lactate and PCr concentration determined in the initial biopsy of individual fish. Points shown on the lower x-axis are mean lactate and PCr levels determined in 11 resting tuna (Table 1). Regressions: $y = -1.28 (\text{PCr}) + 107.9$, $R^2 = 0.93$, and $y = 0.57 (\text{lactate}) + 15.8$, $R^2 = 0.88$.

TABLE 2. Recovery times of PCr and lactate in tuna white muscle

	Recovery time (min)	
	Exercised fish (N = 4)	Nonexercised fish (N = 5)
PCr	79.9 ± 20.9 ^{a,b}	42.4 ± 16.4 ^b
Lactate	76.4 ± 20.3 ^a	42.3 ± 15.2

NOTE: Values are given as means ± SD. Within each test group, PCr recovery time closely matches that of lactate (see also Fig. 5), whereas differences between exercised and unexercised fish were only marginally different.

^a0.07 < p < 0.08 for comparison with nonexercised fish.

^b p > 0.05 for comparison with lactate recovery time.

olism. In some teleosts, in which rates of lactate turnover are greatly mismatched with actual clearance rates from white muscle during recovery from exercise (Milligan and McDonald 1988), retention and utilization of lactate within the white muscle mass is likely the dominant means of lactate disposal. Such a proposal of *in situ* metabolism of muscle lactate is prevalent throughout the area of exercise-recovery metabolism of both mammals and ectotherms. Some evidence comes from Hermansen and Vaage (1977) who biopsied human quadriceps muscle following maximal exercise and point out that the closely matched rates of lactate and glycogen change in muscle, combined with a small arterio-venous difference for lactate, suggest direct reconversion of lactate to glycogen. The enzymic steps involved in the process are not understood well (see Bonen *et al.* 1989 for a partial review), but numerous studies on vertebrate muscle propose varying degrees of *in situ* conversion of lactate to glycogen and demonstrate the dependence of the pathway on muscle fiber type, pH, arterial lactate concentration, and an extramitochondrial pathway of glycogen resynthesis (Bonen *et al.* 1990; Johnson and Bagby 1988; Pagliassotti and Donovan 1990). One proposed pathway involves malic enzyme and phosphoenolpyruvate carboxykinase (Connett 1979). Neither of these enzymes has been

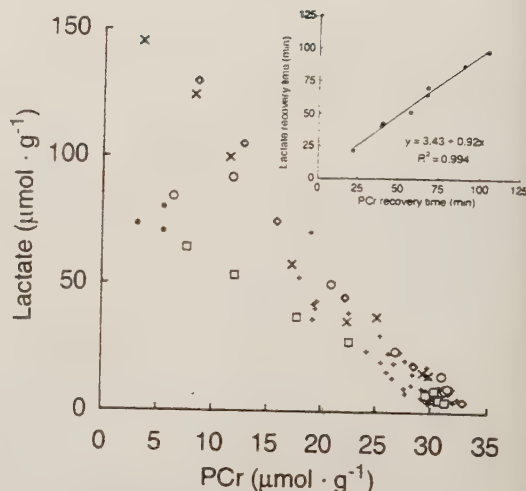


FIG. 6. White muscle lactate in relation to PCr in biopsy samples from exercised (large symbols; each symbol type represents a different fish) and unexercised (small crosses; individuals not depicted) spinally blocked tuna. Also shown are measurements from muscle taken from three fish immediately following 15 min exercise (solid ●). Inset: Estimated lactate recovery time in relation to estimated PCr recovery time for individual fish.

looked for in the white muscle of tuna, but they are present in the white muscle of marlin (Suarez *et al.* 1986).

Results of the present study support and extend the suggestion that tuna white muscle clears lactate *in situ*, since the nearly stoichiometric changes in the lactate and glycogen recovery profiles (i.e., 2 lactate removed : 1 glucosyl unit reformed) indicate mainly a glyconeogenic fate for most of the lactate produced during burst activity. The extent to which this result approaches a quantitative representation of lactate incorporation into white muscle glycogen is reinforced by estimates of minimal glycogenesis from plasma glucose and low capacities for other tuna tissues to utilize lactate (discussed below).

Plasma lactate and glucose: utilization in tuna tissues

Plasma lactate concentration in the exercised tuna remained essentially constant for the period during which muscle lactate declined sharply. In terms of the kinetics of lactate, the restrictive condition of a plasma steady state means that lactate had to enter the plasma pool at the same rate as that at which it was removed. Furthermore, a 35–40 mM level of plasma lactate suggests, indirectly, a high rate of flux through the plasma pool in tuna (see Weber *et al.* 1986). In the postexercise state, white muscle is the probable source of plasma lactate that could be utilized either oxidatively or for gluconeogenesis in other tissues. In mammals, the primarily oxidative disposal of lactate observed at rest and during sustained, aerobic activity has led to the formation of the 'lactate shuttle' hypothesis (Brooks 1986), which proposes the translocation of lactate from producing to consuming muscle fibres.

It is not likely that oxidative metabolism is responsible for the removal of white muscle lactate in tuna. The oxygen consumption of skipjack tuna swimming at 2–5 lengths/s is calculated to be $0.68 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$ (Gooding *et al.* 1981),

which is 4 times the rate in a recovering trout (Milligan and McDonald 1988). This rate of oxygen consumption is still about 30 times too slow to account for the rate of lactate disappearance by oxidation. It is possible that tuna have higher oxygen consumptions during recovery. However, it is unlikely that red muscle or the heart of tuna even have the capacity to oxidize lactate at the rate required. Based on maximal estimates of mitochondrial oxidation of pyruvate, tuna red muscle and heart ventricle could maximally oxidize 0.9 and 2.5 $\mu\text{mol lactate} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$, respectively (Moyes *et al.* 1992). Thus, in a 1-kg animal, red muscle (assume 70 $\text{g} \cdot \text{kg}^{-1}$) could oxidize about 5 mmol of lactate and the heart (4 $\text{g} \cdot \text{kg}^{-1}$, Farrell *et al.* 1992) could oxidize about 0.8 mmol of lactate in 80 min. Combined oxidation in these tissues would therefore account for the removal of less than 10% of an initial white muscle lactate load of 72 mmol (based on 108 $\mu\text{mol} \cdot \text{g}^{-1}$, Table 1). If the temperature of tuna red muscle was 10°C higher than the ambient temperature (Hochachka *et al.* 1978) then maximal oxidation would still account for less than 15% of the lactate clearance.

The low capacity of tuna red muscle to oxidize lactate may mean that red muscle is gluconeogenic to some degree, using lactate derived from white muscle in a manner similar to the version of a lactate shuttle proposed for reptiles (Gleeson and Dalessio 1990). The glycogen content of tuna red muscle is reduced following exhaustive swimming activity (Hulbert *et al.* 1979), but the quantitative importance of lactate incorporation into red muscle glycogen is expected to be low because of the relative masses of red and white muscle. Integration of a shuttling mechanism with the lactate and glycogen changes observed in tuna must accommodate the apparent conservation of lactate carbon within the white muscle mass.

Another way for simultaneous glycogen recovery and lactate disappearance to occur is through the delivery of plasma glucose to muscle for glycogenesis. However, the capacity for skipjack tuna liver to utilize lactate as either a gluconeogenic or an oxidizable substrate is low (Buck *et al.* 1992), and in the general context of postexercise lactate removal, contributes negligibly. Weber *et al.* (1986) came to a similar conclusion by noting that Cori cycle activity is probably minimal in tuna recovering from exercise. While liver glycogenolysis and gluconeogenesis from amino acids are also potential sources of plasma glucose in teleost fishes (Suarez and Mommsen 1987), it remains unlikely that turnover from all of these sources is high enough to supply glucose at a rate that matches the rapid glycogen recovery evident in tuna white muscle. It is generally difficult to predict glucose flux rates because turnover is often independent of plasma glucose concentration (see Bonen *et al.* 1989; Weber *et al.* 1986). However, turnover rate in the present study would have to have been more than an order of magnitude higher than rates measured in tuna by Weber *et al.* (1986), to reflect just 50% repletion of the white muscle glycogen by plasma glucose.

The implication remains that much of the lactate formed during exercise stays in the white muscle or is retrieved from the plasma, and is the principal substrate for glycogen resynthesis. It is interesting that plasma lactate in the exercised tuna declined markedly only after lactate and glycogen recovery in white muscle approached completion. High plasma lactate likely produces a concentration gradient favorable for lactate uptake and utilization by the tissues mentioned above, but may also help to attenuate diffusive efflux of lactate from white muscle. In this regard, tuna resemble those mammals in which

prolonged elevation of plasma lactate seems necessary to sustain *in situ* muscle glyconeogenesis (Johnson and Bagby 1988; Stevenson *et al.* 1987). This is different from the situation in other teleosts, in which plasma lactate is elevated only transiently relative to the prolonged period required for white muscle lactate and glycogen recovery.

There is an apparent inconsistency between the predictably high whole-body lactate turnover rates measured with radio-labeled lactate (see Weber *et al.* 1986) and the proposed intramuscular reconversion of lactate to glycogen. In trout, although plasma lactate kinetics appear unrelated to white muscle glycogen replenishment, there is evidence that an initial outward flux of lactate from white muscle is followed by inward transport to favor metabolism *in situ* (Turner and Wood 1983). A similar kinetic pattern in tuna would mean that whole-body turnover reflects lactate uptake from plasma by the lactate-producing as well as lactate-consuming tissues. Simultaneous lactate extraction and removal has been observed in exercising human leg muscle, in which the extraction of tracer lactate from plasma occurs despite net lactate release by muscle (Stanley *et al.* 1986).

Tuna need to swim continuously and this may mean that muscular contractions in free swimming fish influence changes in lactate and other muscle metabolites, compared with spinally blocked fish. There are no studies of lactate removal from white muscle of free swimming tuna for comparison of methodologies, but the rate of glycogen replenishment in skipjack tuna measured by terminal sampling in recovery from exercise (Barrett and Connor 1964) is comparable to changes in lactate and glycogen measured in the present study. In addition, whereas swimming after intense exercise might change both the rate of lactate clearance from white muscle and whole-body turnover, it is still likely that the principal fate of lactate in tuna is as we have proposed, since the potential to oxidize lactate is low and the proportion of red muscle relative to total muscle mass is small.

The rate of lactate clearance in mammals and tuna is comparable (Weber *et al.* 1986). However, the disposal of lactate appears to be either oxidative (lactate shuttle) or gluconeogenic through the liver (Cori cycle) in mammals whereas neither mechanism seems adequate to explain lactate turnover in tuna. Rather, in tuna, there appears to be a requirement for rapid recovery and, in addition, rapid replenishment of glycogen. Disposal of lactate by oxidative means would require the regeneration of glycogen reserves from food sources, or gluconeogenesis from amino acid precursors. Both of these processes are incompatible with the requirement for rapid replenishment of glycogen. We suggest that glycogen reserves represent a short-term fuel reserved for burst swimming and that by conserving lactate it is possible to conserve glycogen. An analogy can be drawn with the PCr stores, which are available as a short-term energy store that can also be rapidly replenished after exercise. Indeed, the cycle of glycogen to lactate to glycogen is, in a sense, analogous to the cycle of PCr dephosphorylation during exercise and subsequent rapid rephosphorylation in recovery.

Purine nucleotide recovery

Typically, exhaustive exercise in teleosts causes nearly a total depletion of the ATP pool and a stoichiometric increase in IMP (Mommsen and Hochachka 1988; Schulte *et al.* 1992). Recovery patterns vary somewhat, but, as with lactate clearance, a prolonged period is generally required for recovery to

pre-exercise levels. The results presented here for tuna are different in that 15 min of intense swimming caused very little change in the white muscle purine nucleotides of exercised freeze-clamped fish. However, the fish were not exhausted, in the sense of fuel depletion, by the exercise routine employed, and glycolysis and PCR hydrolysis seemed sufficient to protect the ATP concentration. A 50% decrease in ATP content occurred in biopsied fish that were exercised and then anesthetized, but this change was transient and was not evident in freeze-clamped fish that were sampled immediately after exercise. These changes were seemingly caused by the additive effects of the exercise protocol combined with a short-term, more violent struggling action noted upon exposure to the anesthetic. The extent to which the anaesthetic influenced purine nucleotide concentrations independently of exercise-induced changes is not clear, although some effect seems likely, given that MS-222 exposure can cause minor perturbations in white muscle energy status (Van den Thillart *et al.* 1989).

The decline in ATP concentration in the exercised, spinally blocked tuna did not result in a stoichiometric adjustment in the remaining purine nucleotide pool, suggesting that other products of purine metabolism (e.g., adenosine, adenylosuccinate, etc.) probably accumulated. Some purine accumulation in IMP was evident in only the exercised fish, but this was minor considering the size of the phosphorylated adenylate pool. ATP recovered to normal resting levels within 20–40 min after removal of the anesthetic, indicating that the precursors were readily available for adenylate resynthesis. In comparison, trout take up to 24 h to restore ATP concentrations to resting levels. The rapid recovery in tuna ATP levels is consistent with the rapid recovery observed for other metabolites.

Lactate and phosphocreatine

The extraordinary inverse correlation between the concentration of PCr and the concentration of lactate has not, to our knowledge, been previously reported in muscle. Meyer and Terjung (1979) appeared to find a similar relationship between concentrations of PCr and lactate in the recovering gastrocnemius of rats. However, they suggested that the recovery of phosphocreatine was biphasic, whereas the recovery of lactate was fitted best by a single exponential. A comparable relationship between PCr and lactate has also been noted in hypoxic turtle brains (Lutz *et al.* 1984).

We suggest that recovery of intracellular pH (pH_i), dependent on the clearance of lactate, causes the apparent linkage of phosphocreatine to lactate during recovery from exercise in tuna. If, as proposed, lactate is a glyconeogenic substrate, then there would be simultaneous consumption of protons within the white muscle. This suggestion is supported by the work of Tang and Boutilier (1991) who found that protons produced in rainbow trout during intense exercise were most likely cleared by metabolic processes within the white muscle compartment.

A discussed earlier, net efflux seems to account minimally for clearance of lactate from tuna white muscle. Thus, an imbalance, if any, between the clearance of lactate and protons would have only a minimal effect on the relationship between pH_i and lactate. Nevertheless, the efflux of lactate from tuna white muscle may also be linked with proton transport. Lactate and proton movements in muscle appear to be coupled in a carrier-mediated transport process (Mason and Thomas 1988; Juel and Wibrand 1989). Furthermore, lactate transport across

the mammalian sarcolemma is highly sensitive to a pH gradient (Roth and Brooks 1990). It is not clear to what extent these findings can be generalized, as Wiseman *et al.* (1989) found that the efflux of proton and lactate equivalents was not tightly coupled in molluscan muscle tissue. In tuna there is an excess of blood lactate over blood metabolic protons after exercise, but Perry *et al.* (1985) noted that more efficient removal of protons from plasma, rather than differential release of lactate and protons from white muscle, probably accounted for this difference. Directly measuring pH_i and lactate in white muscle would resolve the relationship between the concentrations of protons and lactate. Nevertheless, the evidence is consistent with the suggestion that changes in pH_i are linked with the concentration of lactate.

Phosphocreatine is linked to pH_i through the near equilibrium reaction catalyzed by creatine kinase, where



In addition to pH_i , the ratio of ATP/ADP will also affect the final concentration of PCr. Work on turtle brain and fish white muscle indicates a clear relationship between acidosis, or glycolysis, and PCr depletion induced by hypoxia (Lutz *et al.* 1984; Van Waarde *et al.* 1990). During recovery from anoxia the rephosphorylation of PCr in fish muscle becomes dissociated from recovery of pH_i and presumably lactate clearance. However, during recovery from anoxia there were substantial increases in the ratio of ATP/ADP, which would dissociate pH_i from PCr. Similarly, adenylate ratios seem to influence PCr in rainbow trout white muscle where, in recovery from exhaustive exercise, lactate clearance occurs at a much slower rate than PCr repletion (Schulte *et al.* 1992). The close relationship between lactate and PCr in tuna suggests that changes in pH_i determine the extent of phosphorylation of creatine during recovery. Furthermore, the PCr in tuna white muscle would contribute to the already substantial buffering capacity of this tissue (Castellini and Somero 1981).

Tuna have long been regarded as the elite athletes of the sea, and, in terms of exercise performance, appear to have more similarities with mammals than other teleosts. Certainly, the rates of recovery are more in line with mammalian rates than other teleosts. But there are differences, as tuna appear to have developed a mechanism by which they are not only able to recover from the exercise quickly but are also ready to engage in another burst of high-speed swimming. More direct evidence would be useful in establishing the importance of the proposed glycogen–lactate–glycogen cycle in the white muscle of tuna. In particular, a more extensive correlative analysis of tuna white muscle metabolites, including measurements of pH_i and extracellular pH, would obviously help to delineate the relationships between lactate, PCr, free adenylates, and pH_i during recovery from exercise.

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Seasonal testosterone pattern in Hawaiian monk seals (*Monachus schauinslandi*)

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Summary. Blood samples from four captive male Hawaiian monk seals were collected at intervals of one month for one year for testosterone assay. Plasma testosterone concentrations, measured by radioimmunoassay, revealed a clear seasonal pattern. The lowest mean testosterone concentration (0.09 ± 0.04 ng ml⁻¹) occurred in January, and the highest (1.78 ± 0.40 ng ml⁻¹) in June. The seasonal occurrence of births and of injuries related to mating in wild populations of Hawaiian monk seals showed a distinct association with the period of high testosterone. This study supports other data that indicate that the Hawaiian monk seal is a seasonal breeder and is reproductively active for longer than monachine seals that live in higher latitudes.

Keywords: Hawaiian monk seal; testosterone; seasonal breeding

Introduction

Ecological factors have significantly influenced the evolution of breeding patterns in most animals, including pinnipeds. Two fundamental characteristics of pinniped life history are related to the evolution of their sociosexual behaviour: they are marine feeders and parturition and postnatal pup care must occur on land (Bartholomew, 1970). In addition, reproduction in most pinnipeds is characterized by highly synchronized pupping and mating (Stirling, 1983), as well as delayed implantation of the blastocyst (Fisher, 1954). Most pinnipeds inhabit temperate and polar regions where the combination of delayed implantation and synchronized mating and pupping ensures that the maximum number of offspring are produced at the optimal time of year. Monk seals (*Monachus* spp.) are an exception to this high degree of synchrony.

Monk seals include three species: the Hawaiian monk seal (*Monachus schauinslandi*), the Mediterranean monk seal (*M. monachus*), both of which are endangered, and the extinct Caribbean monk seal (*M. tropicalis*). Monk seals are considered to have evolved from temperate monachine seals of the North Atlantic, with *M. schauinslandi* or its ancestor moving into the Pacific tropics through the then submerged region of Panama during the mid-Miocene (Ray, 1976). The North Atlantic ancestral monachine stock of the monk seal probably exhibited highly synchronized pupping and mating (Stirling, 1983), but millions of years of reduced critical environmental constraints related to reproductive success in the tropical ecosystem appear to have diminished the requirement for this characteristic.

Studies on other phocid seals suggest that seasonal changes in reproductive physiology are directly related to the breeding season. For example, the Southern elephant seal demonstrates seasonal changes in testis weight and spermatogenesis, with the highest testicular weights occurring during the breeding season and the lowest in mid-winter (Griffiths, 1984). Concentrations of plasma testosterone in these seals was increased only during the first month of breeding (Griffiths, 1984).

Captive hooded seals also showed seasonally increased concentrations of plasma testosterone one month prior to the onset of breeding behaviour (Noonan *et al.*, 1991).

Hawaiian monk seals were listed as endangered under the US Endangered Species Act following a 50% reduction in beach counts (Johnson *et al.*, 1982).

With only rare exceptions, the distribution of the Hawaiian monk seal is limited to the Hawaiian Archipelago, and almost all breeding is restricted to the Northwestern Hawaiian Islands. Kenyon & Rice (1959) reported that Hawaiian monk seal pups were born from January until at least the end of June, with most births from mid-March to May. Intensive population monitoring at Laysan Island, one of the primary breeding sites of the Hawaiian monk seal in the northwestern Hawaiian Islands, supports the earlier observation of seasonal breeding (Alcorn, 1984; Johanos *et al.*, 1987; Johanos & Austin, 1988; Alcorn & Buelna, 1989). Monk seal mating is rarely observed because it occurs in the water, probably some distance from shore. However, injuries related to mating (primarily superficial bite wounds and scratches on the dorsal surface of females) are seen seasonally, from April to July at Laysan Island (B. Becker, pers. commun.), and can be used as an indicator of mating activity. This study was based on the hypothesis that, if female Hawaiian monk seals demonstrate seasonal pupping characteristics, a parallel pattern in males should be apparent in concentrations of testosterone in plasma.

Materials and Methods

Animals and blood sampling

Four adult male Hawaiian monk seals were collected as adults at Laysan Island in the Northwestern Hawaiian Islands in May 1987 and housed in a large naturalistic enclosure at Sea Life Park on Oahu, Hawaii (21°N, 158°W). Blood samples were collected at monthly intervals from June 1989 to June 1990, and the animals were observed for signs of moulting. The animals were fed 120–140 mg of the tranquilizer diazepam in their foodfish 2 h before blood collection. Blood was collected from the extradural vein while the seals were physically restrained with netting. Blood samples for testosterone assay were also collected from two wild adult male monk seals at Kure Atoll in the northwestern Hawaiian Islands in June 1990. These two seals were physically restrained and given an intravenous injection of 20 mg diazepam before blood sampling.

Testosterone assay

Testosterone was measured in the plasma using a single antibody radioimmunoassay (Atkinson *et al.*, 1986). The plasma was extracted in 1:10 (v/v) diethyl ether. Extraction recovery was 91.4%. The sensitivity of the assay was 0.05 ng testosterone per tube, and nonspecific binding was 5.5%. A pool of monk seal plasma containing 2.06 ± 0.18 ng testosterone ml⁻¹ was included in each assay to determine interassay variation, which was 11.1%. Log-logit transformations were applied to the standard curve of the assay (Rodbard, 1974).

Data analysis

Data on number of births per month for Hawaiian monk seals from Laysan Island, from 1982 to 1990 (Alcorn, 1984; Johanos *et al.*, 1987; Johanos & Austin, 1988; Alcorn & Buelna, 1989; Johanos *et al.*, 1990), were averaged over 9 years to obtain the mean number of births per month. Data on injuries resulting from mating for Laysan Island, 1988–1990 (Johanos *et al.*, 1990 and B. Becker, pers. commun.), were similarly averaged over 3 years to obtain the mean number of injured animals per month.

Results

A distinct seasonal pattern of circulating concentrations of testosterone was apparent in all four captive seals (Fig. 1). Testosterone concentrations were lowest in January with a mean concentration of 0.09 ± 0.04 ng ml⁻¹, and highest in June with a mean concentration of 1.78 ± 0.40 ng ml⁻¹. Variation among animals increased as they approached the nadir (October–December) and apex (May–June) of the seasonal cycle. All captive seals moulted between mid-October and mid-December. Variation in the daily circulating concentration of plasma testosterone from two seals sampled at 3 h intervals from 08:00 to 17:30 h, was less than 15%, with the highest

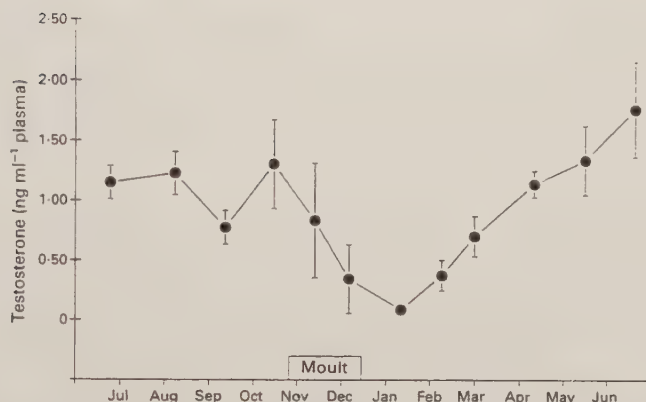


Fig. 1. Plasma concentrations of testosterone (mean $\pm$ SEM) in four adult male Hawaiian monk seals, July 1989 – June 1990.

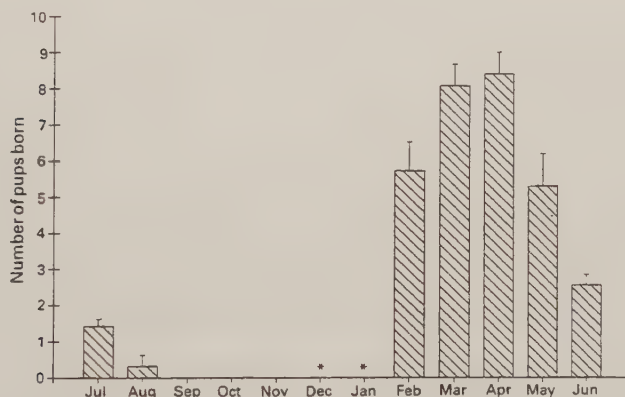


Fig. 2. Numbers (mean $\pm$ SEM) of Hawaiian monk seal pups born per month, 1982–1990, at Laysan Island in the northwestern Hawaiian Islands (data from Alcorn, 1984; Johanos *et al.*, 1987; Johanos & Austin, 1988; Alcorn & Buelna, 1989; Johanos *et al.*, 1990; National Marine Fisheries Service, unpublished). Asterisk indicates a few early-season births that were excluded because the month could not be established with certainty.

concentrations occurring in the afternoon. The plasma testosterone values from the two wild adult males sampled at Kure Atoll in June were 2.70 and 1.59 ng ml⁻¹.

The mean number of births per month at Laysan Island from 1982 through 1990 shows that most pups were born between February and June (Fig. 2). Mating injuries occurred primarily from April to June (Fig. 3).

Discussion

This study demonstrated that the male Hawaiian monk seal has maintained a seasonal, albeit lengthy, breeding trait in a tropical environment (Fig. 1). The nadir of the testosterone concentrations

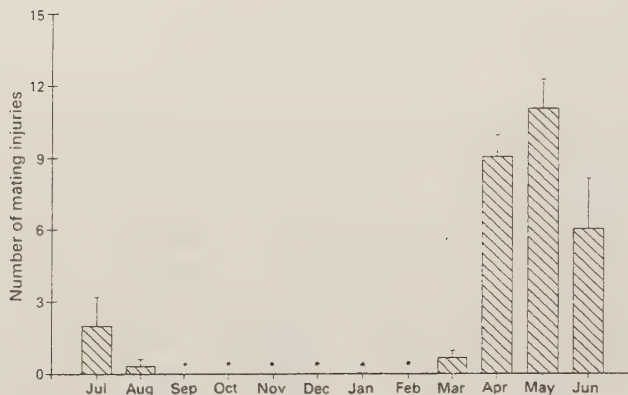


Fig. 3. Numbers (mean $\pm$ SEM) of female Hawaiian monk seals exhibiting mating injuries (scratches and lacerations on mid-back apparently from bites) by month from Laysan Island, 1988–1990 (B. Becker, NMFS Honolulu Laboratory, unpublished). Asterisks indicate that observations were not performed during these months.

occurred in January in all four seals and then steadily increased over the next few months as the seals entered the breeding season. Plasma testosterone remained high through midsummer to autumn and began to decline only after the October sampling, concurrent with the onset of moult. We do not understand why there was a slight depression in the curve in September, which was experienced by all four males, although it is possible that it may be related to pre-moult hormonal changes. This pattern of testosterone concentrations is typically the result of changes in hypothalamic drive that determine pituitary and gonadal function. The higher testosterone concentrations during the breeding season (March–August) reflect increased hypothalamic drive and active spermatogenesis. Low seasonal testosterone concentrations usually indicate reduced, but not necessarily absent, spermatogenesis during the nonbreeding season (October–February). Spermatogenesis usually lags behind testosterone production, as production of testosterone by Leydig cells is necessary for germ-cell differentiation in the tubules of the testes (Turner & Bagnara, 1976). This time lag varies with species but is generally of the order of 3–8 weeks. If this time lag is applied to the testosterone concentrations (Fig. 1), the spermatogenic cycle could be estimated for this species.

The seasonal cycle of testosterone secretion found in these captive males is also consistent with the observed pattern of births and breeding-induced wounds observed in the wild. Pupping occurs over 6 months with the greatest percentage being born from March through May. The seasonal pattern of mating is more difficult to define, as it is not possible to identify accurately when copulation takes place. However, high testosterone concentrations occurred during the time that mating-induced wounds were observed on mature females. When these patterns are compared with other monachine seals, it appears that, although the Hawaiian monk seal has maintained a seasonal pattern of breeding, the length of the breeding season has been extended compared with related species in higher latitudes. The monachine subfamily of seals is found in a broad range of habitat types and its breeding seasons are similarly varied. The high-latitude Antarctic crabeater seal (*Lobodon carcinophagus*) and Weddell seal (*Leptonychotes weddelli*) give birth and mate within 3–4 weeks; the more temperate climate monachines (*Mirounga* spp.) show a less temporally confined pattern of 4–8 weeks, and the monk seals (*Monachus* spp.) in their low-latitude habitats have a broad temporal distribution of pupping and breeding over at least 6 months (Stirling, 1983). The prolonged pattern of high testosterone concentrations is consistent with the extended pupping season, as it allows for females that may give birth late to be bred in the same season.

A major concern in using captive individuals in this study was whether the endocrine system may have been suppressed in the captive environment. The testosterone values from two wild adult male seals sampled at Kure Atoll in June are within the measured range of the captive monk seals at the same time of year. This indicates that the high testosterone concentrations in the cycle exhibited by the captive monk seals is probably representative of circulating testosterone concentrations in wild adult male monk seals.

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Sulfide-hemoglobin interactions in the sulfide-tolerant salt marsh resident, the California killifish *Fundulus parvipinnis*

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Summary. Sulfide can potentially damage hemoglobin or be detoxified by hemoglobin. In the sulfide-tolerant California killifish neither seems to be the case at environmentally realistic (micromolar) and physiologically relevant (millimolar) sulfide concentrations. An 8-h exposure of killifish to 5 and 8 mmol sulfide $\cdot$ l $^{-1}$ results in 50–100% mortality, but not due to sulfhemoglobin (where sulfide covalently binds to the porphyrin) nor ferric hemoglobin (Hb $^{+}$), both dysfunctional hemoglobin derivatives. Killifish hemoglobin converts to sulfhemoglobin in vitro only in the presence of 1–5 mmol sulfide $\cdot$ l $^{-1}$. The amount of sulfhemoglobin formed increases with time and heme concentration but decreases with pH. Hb $^{+}$ binds sulfide as ferric hemoglobin sulfide (Hb $^{+}$ S, an unstable complex where sulfide ligates to the iron), and also as sulfhemoglobin. Killifish blood does not catalyze the oxidation of 10–500 μ mol sulfide $\cdot$ l $^{-1}$ to any appreciable extent. Radiolabeled sulfide incubated with oxyhemoglobin or whole blood disappears at rates greater than in buffers, but only minimal amounts of thiosulfate and no sulfate nor sulfite are formed (elemental sulfur and bound sulfide not quantified). Sulfide disappearance rates increase linearly with initial sulfide concentration. Hb $^{+}$ does catalyze the oxidation of sulfide to thiosulfate in vitro. Similar experiments on another sulfide-tolerant species, the long-jawed mudsucker *Gillichthys mirabilis*, produced similar results.

Key words: Sulfhemoglobin – Sulfide oxidation – Blood – Sulfide tolerance – Cyprinodontidae

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Abbreviations: ANOVA, analysis of variance; BV, benzyl viologen; HEPES, *N*-2-hydroxyethylpiperazine-*N'*-2-ethanesulfonic acid; HPLC, high-pressure liquid chromatography; RBC, red blood cells; SHb, sulfhemoglobin

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Introduction

Hemoglobin and sulfide affect one another in several ways, and the interaction has been examined from different points of view. One is the impairment of O $_2$ transport due to the formation of SHb, a derivative with lower O $_2$ affinity (Carrico et al. 1978a, b; Wells and Pankhurst 1980). Another is the amelioration of sulfide toxicity by the blood. The blood has been implicated in sulfide metabolism, oxidation and detoxication in dogs, rats and cats (Haggard 1921; Sörbo 1958; Evans 1967; Curtis et al. 1972; Bartholomew et al. 1980), marine worms (Patel and Spencer 1963b; Powell and Arp 1989; Vismann 1990) and marine fishes (Bagarinao and Vetter 1989). Also, the immobilization or binding of sulfide to ferrous and ferric hemoglobin or other blood proteins reduces toxicity (Smith and Gosselin 1964, 1966; Smith et al. 1977; Torrains and Clemens 1982), or sulfide may be transported to internal bacterial symbionts (Arp et al. 1984, 1985, 1987). It should be noted that the above categories are not mutually exclusive. SHb formation is a form of immobilization, where sulfide adds across a pyrrole double bond in the porphyrin as an episulfide (Morell et al. 1967; Nichol et al. 1968; Berzofsky et al. 1972; Brittain et al. 1982). Formation of ferric hemoglobin-sulfide complex likewise immobilizes sulfide, but the complex is unstable and eventually yields an oxidized sulfur product (Coryell et al. 1937).

The major site of sulfide toxicity is cytochrome c oxidase, which is inhibited by sulfide at nanomolar to low micromolar levels (National Research Council 1979; Bagarinao 1992). If hemoglobin readily converts to SHb in the presence of sulfide, O $_2$ transport stops and sulfide toxicity is aggravated. However, if hemoglobin has sufficiently high binding and/or oxidation capacity for sulfide, such that it can rapidly bring the free sulfide concentration to low nanomolar levels, then it can potentially "protect" cytochrome c oxidase.

This paper describes experiments on the California killifish *Fundulus parvipinnis*, and to a lesser extent the long-jawed mudsucker *Gillichthys mirabilis* to determine

the role of hemoglobin in aggravating or ameliorating sulfide toxicity. These two species are remarkably tolerant to sulfide and experience potentially high levels of sulfide (millimolar levels in sediment pore water, micromolar levels in the water column) in their salt marsh habitat (Bagarinao and Vetter 1989; Vetter et al. 1989; Bagarinao 1991). Bagarinao and Vetter (1989) found that the blood of these two species, as well as several other marine fishes, had high sulfide-oxidizing activity, based on a spectrophotometric assay using the artificial electron acceptor BV (Powell and Somero 1985). In addition, sulfide-exposed fishes contained low sulfide and high thiosulfate concentrations in the tissues, indicating that sulfide was oxidized and detoxified *in vivo*. Thiosulfate concentrations were highest in the blood. These results raised the question of whether the blood itself oxidized sulfide to thiosulfate or simply acted as depot for thiosulfate formed elsewhere. For example, thiosulfate was produced by liver mitochondria incubated with radiolabeled sulfide (Bagarinao and Vetter 1990).

The specific questions addressed in the present study are: (1) Is fish mortality during acute sulfide exposure due to SHb formation? (2) Does sulfide bind to hemoglobin and form SHb *in vitro*; what factors affect SHb formation? (3) Does fish blood, specifically oxyhemoglobin and ferric hemoglobin, catalyze sulfide oxidation? At least for the California killifish and the long-jawed mudsucker, the answers are essentially negative at environmentally realistic and physiologically relevant sulfide concentrations: the blood neither aggravates nor ameliorates sulfide toxicity. Our results are important for the contrasts and clarification they provide relative to previous studies.

Materials and methods

Exposure of fish to sulfide. The killifish and the mudsucker were exposed to relatively high concentrations of sulfide to determine the acute lethal level and to see whether changes in the blood accompany mortality of fish. Newly caught fish from the salt marsh were exposed to sulfide in flow-through aquaria (Bagarinao and Vetter 1989). Duplicate aquaria were stocked with 12 killifish each and sulfide was delivered to achieve constant concentrations of 0.2, 1, 2, 5 and 8 mmol $\cdot$ l $^{-1}$ for 8 h, with controls not receiving any sulfide. The long-jawed mudsucker was tested only at 2 and 5 mmol $\cdot$ l $^{-1}$ sulfide. At 2-h intervals three fish were removed from one aquarium and examined for hemoglobin spectra.

Preparation of hemolysates. The California killifish were small and yielded only 30–100 μ l blood per fish. Blood was taken from individual fish by cutting off the tail with a scalpel and allowing the blood to drain into heparinized capillary tubes or directly into a cuvette containing a buffer with 290 mmol NaCl $\cdot$ l $^{-1}$, 1 mmol TRIS $\cdot$ l $^{-1}$, pH 7.35, and 64 USP-STK-1 units heparin $\cdot$ ml $^{-1}$ [method modified from Riggs (1981)]. After stirring, a spectral scan was immediately made of each whole blood suspension. These suspensions were always turbid but showed typical oxyhemoglobin spectra. Each blood sample was then transferred from the cuvette to a microfuge tube and spun at 13 000 $\times$ g for 2 min to pellet the RBC from the plasma proteins. The pellet was resuspended in buffer with 150 mmol NaCl $\cdot$ l $^{-1}$, 1 mmol TRIS $\cdot$ l $^{-1}$, pH 7.35 and no heparin, then washed by spinning for 2 min. The RBC were lysed in distilled water, then spun again for 2 min to pellet membranes. The clear hemolysates were then used for spectral scans (within

10 min of blood withdrawal), sulfide-binding experiments, and sulfide oxidation assays. Some hemolysates were left to autoxidize in the refrigerator (5 $^{\circ}$ C) and used 2 weeks later for *in vitro* experiments with ferric hemoglobin.

Heme concentration was determined by adding known volumes of hemolysates to 2 ml Drabkin's reagent (1 g NaHCO₃, 0.2 g K₄[Fe(CN)₆], 0.05 g KCN in 1 l distilled water, plus 0.5 ml BRIJ 35; Sigma assay kit #525), waiting for 5 min and reading the absorbance of the ferric hemoglobin-cyanide derivative at 540 nm. Heme (mmol $\cdot$ l $^{-1}$) was calculated using the extinction coefficient 11 mmol $^{-1}$ $\cdot$ l $\cdot$ cm $^{-1}$ (Salvati and Tentori 1981) and allowing for the dilution of the hemolysates.

Spectral scans of hemolysates. Scans were made at the wavelength range 375–675 nm using a Perkin-Elmer Lambda 4A spectrophotometer with software from Softways (Moreno Valley, CA, USA). Distilled water and all buffers used in the scans had a flat absorbance of about 0.037 (which was corrected for) throughout this wavelength range. All scans were done at 20 $^{\circ}$ C. In these scans, the particular form of hemoglobin was noted: ferrous oxyhemoglobin (oxyHb, with bands at 540 and 576 nm in addition to the Soret band), ferrous deoxygenated (Hb, with single band at 555 nm), ferric hemoglobin or methemoglobin (Hb⁺, with bands at 500 and 630 nm), ferric hemoglobin-sulfide or sulfmethemoglobin (Hb⁺S, with band at 545 nm and a shoulder at 575 nm), ferrous sulfhemoglobin (SHb, with band at 613–623 nm, depending on ligand), ferric sulfhemoglobin (SHb⁺, with bands at 590 and 715 nm at pH 5.5 or 620 and 665 nm at pH 10), denatured ferric hemechrome (with bands at 535 and 565 nm), or denatured ferrous hemechrome (with bands at 527 and 557 nm) based on the literature [summarized by Salvati and Tentori (1981); Tentori and Salvati (1981)]. SHb spectra, ferric and ferrous, with and without various ligands, appear in several papers (van Assendelft 1970; Dijkhuizen et al. 1977; Carrico et al. 1978b; Brittain et al. 1982). Spectra of Hb⁺S are shown by Keilin (1933), Doeller et al. (1988) and Kraus and Wittenberg (1990).

In the present study, SHb formation was monitored as the ratio of the absorbance at 618 nm and the absorbance at 576 nm (A_{618}/A_{576}), based on the observation that in the presence of sulfide the 576-nm band decreased as the 618-nm band increased. This relative measure was necessitated by the large numbers of samples that had to be scanned and assessed promptly. The purity and concentration of SHb solutions may be determined using the ratio $A_{620}/A_{580} = 2.6$ for a 100% pure deoxygenated SHb sample, and an extinction coefficient of 21.5 mmol $^{-1}$ $\cdot$ l $\cdot$ cm $^{-1}$ at 620 nm (Nichol et al. 1968; Carrico et al. 1978b; Brittain 1981). Marchant et al. (1974) used A_{620}/A_{561} , with ratios greater than 2 indicating 80% purity or better. Other methods of SHb measurement have also been described by Evelyn and Malloy (1938) and Dijkhuizen et al. (1977).

A few observations were made of the *in vitro* reaction of sulfide with killifish Hb⁺ to form Hb⁺S. Hb⁺S was never observed in sulfide-exposed killifish or mudsucker, and the assays were made mostly for comparison with the literature.

Assays of sulfhemoglobin formation and sulfide binding *in vitro*. The effects of sulfide on hemoglobin spectra and SHb formation *in vitro* were determined in the California killifish, long-jawed mudsucker and three other marine fishes. In the killifish experiments, a hemolysate was prepared from the RBC of five individuals and assayed for heme content. An appropriate volume of hemolysate was added to either distilled water (pH around 6.7) or saline buffer (150 mmol NaCl $\cdot$ l $^{-1}$, 1 mmol TRIS $\cdot$ l $^{-1}$, pH 7.35) in a cuvette to achieve the same concentration of 30 μ mol heme $\cdot$ l $^{-1}$ in all spectral assays. Stock solutions of sulfide were added in microliter amounts to the cuvettes to achieve various concentrations from 0.2 to 15 mmol $\cdot$ l $^{-1}$. Spectral scans were made at different times up to 1 h following sulfide addition, with different heme concentrations (30, 60, 90 and 120 μ mol $\cdot$ l $^{-1}$) in the cuvette, and at different pH. In the pH experiment, buffer containing (mmol $\cdot$ l $^{-1}$) 150 KCl, 25 potas-

sium phosphate and 20 HEPES and adjusted to 0.5 pH unit intervals between pH 6.5 and pH 8.0 was used. After addition of aliquots of hemolysate, the new pH was determined prior to the spectral scans.

In a related sulfide-binding experiment, hemoglobin samples of 3–4 ml in dialysis tubings were immersed in 11 50 mmol HEPES $\cdot$ l $^{-1}$ (pH 7.4) with 1 mmol sulfide $\cdot$ l $^{-1}$ initial concentration for 12 h at 5°C (without stirring), and in another run for 24 h at room temperature (with stirring). Spectral scans and heme determinations were made of these samples before and after the immersion period. The samples were then dialyzed in 20 mmol HEPES $\cdot$ l $^{-1}$ (pH 7.4) for 24 h and the spectra again determined. Duplicate samples of blood and buffers were analyzed by the (monobromo)bimane-HPLC method (Vetter et al. 1987, 1989). Sulfate and elemental sulfur were not determined.

Assays of sulfide oxidation by blood. Initial studies of sulfide oxidation by blood and blood components were made using BV in an indirect assay where the rate of BV reduction was assumed to be proportional to sulfide oxidation (Powell and Somero 1985). The assay used 5 mmol sulfide $\cdot$ l $^{-1}$ and 2 mmol BV $\cdot$ l $^{-1}$ under anaerobic conditions at pH 9.0. In one experiment, plasma, RBC and membrane fractions were made from walleye surfperch *Hyperprosporon argenteum* (a large-sized species that yielded good amounts of blood). All the activity was found in the hemolysate fraction. In another experiment, 13 RBC hemolysates from individual California killifish were assayed and the relationship between the rates of BV reduction (= sulfide oxidation?) and heme concentrations was determined.

To determine whether fish hemoglobin can remove sulfide from free solution at fast enough rates under near-physiological conditions (without BV, with O₂, lower sulfide concentrations, and at pH 6.7–7.4 in vitro), time-series assays were done on RBC hemolysates prepared from killifish and mudsucker. In the low-sulfide assays, samples were placed in an all-glass chamber with an O₂ electrode. In each assay, either radiolabeled (³⁵S) or unlabeled sulfide was added in microliter amounts to achieve concentrations between 10 and 500 μ mol $\cdot$ l $^{-1}$ in a reaction volume of 1.0–1.5 ml. Then, 100- μ l aliquots were withdrawn by Hamilton syringe after 0, 2, 5, 10, and 15 min, fixed in 10 mmol bimane $\cdot$ l $^{-1}$ and analyzed for sulfide and its oxidation products by HPLC with fluorescence detection and on-line scintillation counting (Vetter et al. 1987, 1989).

Killifish hemolysates were made from single fish or pooled from 2–5 fish. Only 2–4 time-series assays at different sulfide concentrations could be done on any hemolysate sample. A total of 22 assays were made of oxyHb in 14 hemolysate samples from 20 killifish, and 7 assays of Hb⁺ in 5 samples from 5 fish. Three assays were made of a sample of mudsucker oxyHb. For each assay, the concentrations of sulfide and its oxidation products were plotted against time, and linear regressions were fitted to obtain rates from the slopes (μ mol $\cdot$ l $^{-1} \cdot$ min $^{-1}$, recalculated as nmol $\cdot$ min $^{-1}$). The rates were normalized to nanomoles heme in the assays, then to milligrams Hb (1 nmol heme = 0.016 mg Hb) to account for differences in heme concentration in the assays. Rates were then plotted against initial sulfide concentration to determine the kinetics, analogous to enzyme-catalyzed reactions where rates are analyzed as a function of substrate concentration.

Whole blood of killifish (pooled from 15 individuals) was also assayed for oxidation of high concentrations of sulfide in 2-ml heparinized glass vials at room temperature (about 20°C) without stirring. Radiolabeled sulfide was added to 250 μ l blood or NaCl buffer control to a concentration of 5 mmol $\cdot$ l $^{-1}$ (this concentration being acutely lethal to the killifish and the one used in the BV assay). Aliquots of 50 μ l reaction mixture were fixed at 0, 2, 5 and 10 min, and analyzed by the bimane-HPLC method.

Statistical analysis. Where appropriate, data and treatments were analyzed for statistical significance by Student's *t*-test, ANOVA, and Tukey's test, according to Zar (1984). Figures were drawn by the Cricket Graph computer program.

Results

SHb (non-formation) in fish exposed to sulfide

No killifish died in the control or exposure treatments at concentrations between 0.2 and 2 mmol sulfide $\cdot$ l $^{-1}$. However, 50% of killifish exposed to 5 mmol sulfide $\cdot$ l $^{-1}$ died in 6–8 h, and all died in 2–4 h in 8 mmol sulfide $\cdot$ l $^{-1}$. Among the mudsuckers, 50% died in 4–6 h in 5 mmol sulfide $\cdot$ l $^{-1}$, and 17% succumbed in 2 mmol sulfide $\cdot$ l $^{-1}$. Exposure of killifish to sulfide at all concentrations up to 8 mmol $\cdot$ l $^{-1}$ in seawater for 2–8 h did not result in the formation of high levels of SHb, nor any other hemoglobin derivative such as Hb⁺ and Hb⁺S. Almost all hemolysates showed strong alpha (576 nm), beta (540) and Soret (413 nm) bands typical of oxyHb, except those of two killifish and three mudsuckers. The two killifish with SHb were an individual that died after 6 h in 5 mmol sulfide $\cdot$ l $^{-1}$ (A_{618}/A_{576} ratio = 0.142), and an individual still alive after 6 h in 2 mmol sulfide $\cdot$ l $^{-1}$ (ratio = 0.172). Seven others that died in 5 mmol sulfide $\cdot$ l $^{-1}$ did not have SHb in the bloodstream. In the 8 mmol sulfide $\cdot$ l $^{-1}$ treatment, 12 dead fish showed no SHb probably because death was more immediate. The two mudsuckers with SHb died in 4–6 h in 2 mmol sulfide $\cdot$ l $^{-1}$. No mudsucker in 5 mmol sulfide $\cdot$ l $^{-1}$ was examined for SHb. These data indicated that SHb was not formed in significant amounts during in vivo sulfide exposure, and that death of fish during the experiments was not due to SHb. Control killifish showed A_{618}/A_{576} ratios of 0.024 ± 0.017 (mean $\pm$ SD, $n=25$), and sulfide-exposed

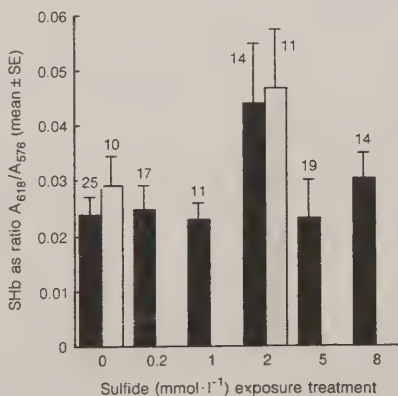


Fig. 1. Sulfhemoglobin (SHb) levels as ratio A_{618}/A_{576} in *Fundulus parvipinnis* (black bars) and *Gillichthys mirabilis* (stippled bars) exposed to different sulfide treatments. Bars show mean $\pm$ SE, with sample sizes indicated. Samples from each treatment include fish bled at 2, 4, 6 and 8 h (no significant difference between sampling periods). All fish from the controls and the 0.2, 1 and 2 mmol sulfide $\cdot$ l $^{-1}$ treatments were alive; 50% of those from 5 mmol sulfide $\cdot$ l $^{-1}$ and 75% of those from 8 mmol sulfide $\cdot$ l $^{-1}$ were dead at sampling. No significant difference in mean SHb levels with sulfide concentration (one-way ANOVA, $F=1.685$, $p>0.05$).

fish had mean ratios not significantly different from the controls (Fig. 1). No significant difference was found in SHb levels with duration of exposure from 2 to 8 h. In another study, killifish exposed to 200 μM sulfide for 4 days had SHb levels of 0.026 ± 0.012 ($n=12$).

Although the activity of cytochrome c oxidase was not assayed during the above experiment, it was highly likely that inhibition of the enzyme was responsible for the mortality observed in 2–5 mmol sulfide $\cdot \text{l}^{-1}$ over 4–8 h. In a separate experiment, exposure of killifish to 700 μM sulfide $\cdot \text{l}^{-1}$ caused significant inhibition (50–90% over 2–72 h) of cytochrome c oxidase in the gill and brain (Bagarinao 1991).

Effects of sulfide on fish hemoglobin *in vitro*

Spectral changes. Hemoglobin solutions of the California killifish, long-jawed mudsucker and three other species of fish showed absorbance spectra typical of vertebrates and were affected by sulfide in the same manner. In no case was Hb^+ nor Hb^+S generated when sulfide was added to oxyHb. Instead, when the spectral assays were done at pH 6.5–7.0, with 30 μM heme $\cdot \text{l}^{-1}$ and after 5 min of sulfide addition, absorbance at the alpha, beta and Soret bands decreased with increasing concentrations of sulfide between 0.02 and 10 mmol $\cdot \text{l}^{-1}$. The reductions in absorbance were steeper at concentrations greater than 1 mmol sulfide $\cdot \text{l}^{-1}$. The decreases of the alpha and beta bands were on the order of 0.01 absorbance units per mmol sulfide $\cdot \text{l}^{-1}$. The absorbance at 618 nm, indicative of SHb formation, increased very slightly (0.01 absorbance unit per mmol sulfide $\cdot \text{l}^{-1}$) through three orders of magnitude increase in sulfide concentration and became noticeable only at greater than 1 mmol $\cdot \text{l}^{-1}$. Figure 2A shows four spectra of killifish hemoglobin with increasing A_{618} .

In the presence of (excessive) 15 mmol sulfide $\cdot \text{l}^{-1}$, hemoglobin became deoxygenated within 2–5 min, its absorbance band shifting to 555 nm. This was immediately followed by denaturation, with the bands shifting to 527 and 557 nm (hemochrome, Fig. 2B), and the Soret band coming back up. A hemochrome also formed after about 10 min in 10 mmol sulfide $\cdot \text{l}^{-1}$. The hemochrome bands increased while the absorbance at 618 nm decreased with time. No hemochrome was formed in sulfide up to 1 mmol $\cdot \text{l}^{-1}$.

The spectral changes caused by sulfide were different from those caused by cyanide and nitrite at the same 10 mmol $\cdot \text{l}^{-1}$ concentration (Fig. 2C). Cyanide had little effect on oxyHb spectra. Nitrite produced Hb^+ as expected. Addition of cyanide to SHb did not eliminate A_{618} .

Sulfhemoglobin formation *in vitro*. Red hemoglobin solutions with 1–5 mM sulfide turned green with time and showed increasingly larger bands at 618 nm. SHb levels expressed as the ratio A_{618}/A_{576} increased with sulfide concentration, time, and heme concentration, and decreased with pH (Fig. 3). OxyHb (30 μM heme $\cdot \text{l}^{-1}$) in distilled water (pH 6.75) formed SHb in 5 min only in the presence of sulfide concentrations in excess of

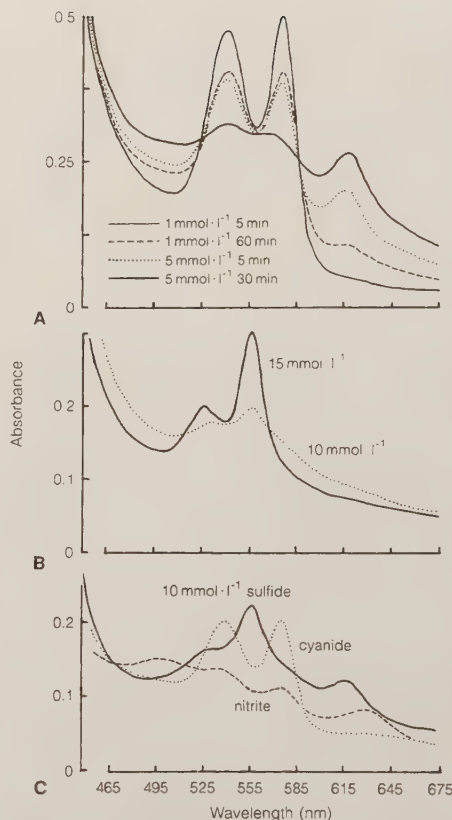
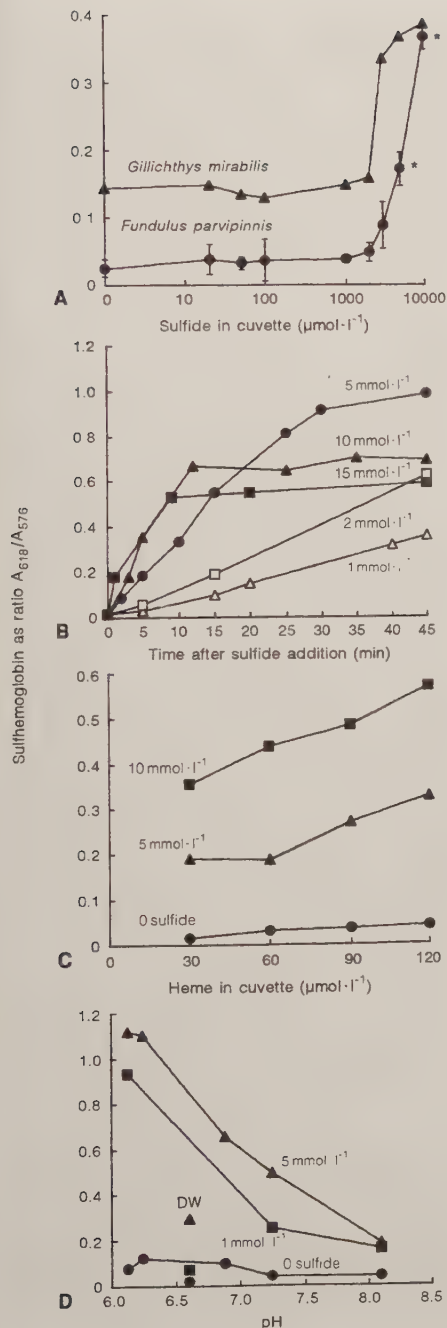


Fig. 2A–C. Spectral changes in California killifish hemoglobin following addition of sulfide. A In the presence of 1 mmol sulfide $\cdot \text{l}^{-1}$ after 5 min (thin solid line), 60 min (dashed line), 5 mmol sulfide $\cdot \text{l}^{-1}$ after 5 min (dotted line), and 30 min (bold solid line). Note decrease in absorbance at 540 nm and 576 nm and increase in absorbance at 618 nm, indicative of sulfhemoglobin (SHb). The Soret peak also decreases but is omitted in figure. The spectrum for 1 mmol $\cdot \text{l}^{-1}$ sulfide at 5 min differs little from that of the control hemolysate, i.e., typical oxyhemoglobin. B In the presence of 10 and 15 mmol sulfide $\cdot \text{l}^{-1}$, hemoglobin is deoxygenated (a single peak at 555 nm momentarily appears), then becomes denatured, i.e., a hemochrome is formed with absorbance at 527 nm and 557 nm. C The effect of sulfide on hemoglobin differs from that of cyanide and nitrite at the same 10 mmol $\cdot \text{l}^{-1}$ concentration. All scans were made of hemolysates with 30 μM heme $\cdot \text{l}^{-1}$ in distilled water pH 6.7.

1 mmol $\cdot \text{l}^{-1}$. This was true for the five species of fish examined, only two being shown in Fig. 3A. At any sulfide concentration, SHb levels increased with time, and more rapidly in high sulfide (Fig. 3B). At 5 mmol sulfide $\cdot \text{l}^{-1}$ an asymptote SHb level was reached in 45 min near a ratio of 1.0. At 10 and 15 mmol sulfide $\cdot \text{l}^{-1}$, SHb ratios remained near 0.6 due to the onset of denaturation and hemochrome formation. Given



enough time, sulfide at concentrations less than $1 \text{ mmol} \cdot \text{l}^{-1}$ also produced SHb. For example, in one hemolysate, $500 \mu\text{mol sulfide} \cdot \text{l}^{-1}$ produced SHb of ratio 0.5 in 2 h (not shown).

In the presence of 5 and 10 mmol sulfide $\cdot \text{l}^{-1}$, more SHb formed with more hemoglobin (Fig. 3C), 120 $\mu\text{mol heme} \cdot \text{l}^{-1}$ being the upper limit for spectrophotometric resolution and about 1/20 of the heme concentration of whole blood. Samples with 30, 60, 90 and 120 $\mu\text{mol heme} \cdot \text{l}^{-1}$ and 5 mmol sulfide $\cdot \text{l}^{-1}$, fixed in bismine after being scanned at 5 min, showed 1774, 1565, 1443 and 925 $\mu\text{mol sulfide} \cdot \text{l}^{-1}$, and 98, 61, 52 and 57 $\mu\text{mol thiosulfate} \cdot \text{l}^{-1}$, respectively (data not shown). Although these were single determinations they suggested that more heme bound more sulfide, such that less sulfide was oxidized to thiosulfate or was free and available to bismine binding.

Finally, acid pH favored SHb formation (Fig. 3D), with greater amounts being formed in KCl buffer than in distilled water at the same pH. The SHb values plotted in Fig. 3A–C were of hemolysates in distilled water of pH around 6.7 and probably underestimated SHb formation under KCl-buffered conditions.

Reaction of sulfide with ferric hemoglobin. California killifish hemoglobin autoxidized in the refrigerator at a rate of about 3% per day. Addition of 50, 100, 500, and 1 mmol sulfide $\cdot \text{l}^{-1}$ to Hb^+ resulted in the immediate (within 1 min) appearance of Hb^+S , a band at 540–541 nm with a shoulder at 574–576 nm, and the reduction or disappearance of the characteristic band of Hb^+ at 630 nm. At the two lower concentrations (50 and 100 $\mu\text{mol sulfide} \cdot \text{l}^{-1}$), Hb^+S dissociated within 30 min back to Hb^+ with the band at 630 nm. At the two higher concentrations Hb^+S dissociated more slowly, and a band at 616–618 nm, indicative of SHb, appeared and became stronger with time. Figure 4 shows spectra of Hb^+ before addition of sulfide, and Hb^+S formed 1 min, 30 min and 1 h after addition of 1 mmol sulfide $\cdot \text{l}^{-1}$ to Hb^+ . Addition of dithionite caused a shift to typical alpha and beta bands (i.e., reduction of Hb^+) and persistence of the SHb band. Cyanide at 1–10 mmol $\cdot \text{l}^{-1}$ converted Hb^+ to Hb^+CN with a band at 540 nm.

Fig. 3A–D. Sulfhemoglobin formation in vitro in California killifish hemolysates, expressed as the ratio A_{618}/A_{576} , as a function of various factors: **A** sulfide concentration (note that scale is logarithmic); **B** time after sulfide addition; **C** heme concentration; and **D** pH. All scans were made 5 min after sulfide addition except in **B**, with 30 $\mu\text{mol heme} \cdot \text{l}^{-1}$ except in **C**, in distilled water (DW) pH 6.7 except in **D**. For interspecies comparison, a curve for the long-jawed mudsucker is also given in panel **A**; panels **B–D** are for the killifish only. Variability between two hemolysate preparations (each preparation from 5 killifish) is indicated by the mean $\pm \text{SD}$ curve in panel **A**. Asterisks indicate significantly high SHb values at 5–10 mmol sulfide $\cdot \text{l}^{-1}$ (ANOVA, $F=52.83$, $p<0.005$ and Tukey's test, q values of $P<0.05$). All other points plotted are from single scans. Inter-scan variability about 5–6% for the same sample and same treatment. The results in **B** are duplicated for other species (not plotted). **C** is from one hemolysate, and **D** is a composite of two hemolysates

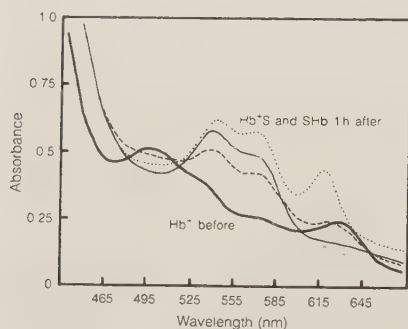


Fig. 4. Effect of sulfide on ferric hemoglobin (Hb^+) in vitro. Addition of $1 \text{ mmol sulfide} \cdot \text{l}^{-1}$ to Hb^+ with the band at 630 nm (bold solid line) produces ferric hemoglobin sulfide (Hb^+S) and no sulfhemoglobin (SHb) in 1 min (thin solid line). With time, the SHb band at 618 nm appears (30 min, broken line) and becomes stronger (1 h, dotted line)

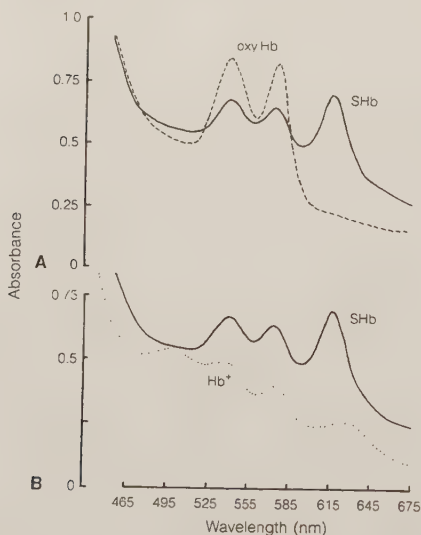


Fig. 5A, B. Sulfhemoglobin (SHb) formation in California killifish hemolysates incubated for 12 h in $1 \text{ mmol sulfide} \cdot \text{l}^{-1}$ at 5°C . A Ferrous oxyhemoglobin (oxyHb) at the start, converted to SHb 12 h later. B Ferric hemoglobin (Hb^+) at the start, converted to SHb 12 h later. Dialysis of the SHb samples for 24 h does not remove the bound sulfide

Sulfide binding. The hemolysates of both killifish and mudsucker bound sulfide as SHb but did not concentrate it. Immersion of dialysis tubings with hemolysates in $1 \text{ mmol sulfide} \cdot \text{l}^{-1}$ for 12 h at 5°C without stirring resulted in solutions with less than equilibrium concentrations of sulfide, around $500 \mu\text{mol} \cdot \text{l}^{-1}$ instead of greater than $700 \mu\text{mol} \cdot \text{l}^{-1}$ as in the buffers (Table 1, middle panel). More thiosulfate appeared in the Hb^+ sample

Table 1. Results of the sulfide-binding experiment on fish blood. Sulfhemoglobin levels are given as the ratio A_{618}/A_{576} . See text for explanation of oxyHb2

Blood sample	pH	Heme ($\mu\text{mol} \cdot \text{l}^{-1}$)	A_{618}/A_{576} ratio	Sulfide ($\mu\text{mol} \cdot \text{l}^{-1}$)	Thiosulfate ($\mu\text{mol} \cdot \text{l}^{-1}$)
At start of immersion in $50 \text{ mmol HEPES} \cdot \text{l}^{-1}$ buffer, pH 7.4, with $1 \text{ mmol sulfide} \cdot \text{l}^{-1}$					
<i>Fundulus parvipinnis</i>					
OxyHb	7.22	132	0.24		
Hb^+	6.75	113	0.59		
OxyHb 2	7.30	168	0.06		
<i>Gillichthys mirabilis</i>					
OxyHb	6.77	170	0.12		
Buffer bath (with sulfide)				925	116
Buffer tubing (without sulfide)				0	0
After 12 h immersion in buffer with sulfide at 5°C without stirring					
<i>F. parvipinnis</i>					
OxyHb	7.45	94	1.04	448	230
Hb^+	7.48	108	1.08	545	337
OxyHb 2	nd	nd	1.00		
<i>G. mirabilis</i>					
OxyHb	7.45	115	0.70	454	204
Buffer bath (with sulfide)				793	200
Buffer tubing (with sulfide)				727	204
After 24 h dialysis in $20 \text{ mmol HEPES} \cdot \text{l}^{-1}$ buffer, pH 7.4, at 5°C without stirring					
<i>F. parvipinnis</i>					
OxyHb	7.30	91	0.88	43	131
Hb^+	7.35	nd	0.89	44	153
OxyHb 2	nd	nd	0.88		
<i>G. mirabilis</i>					
OxyHb	7.27	nd	0.70	34	129
Buffer bath (without sulfide)				1	139
Buffer tubing (with sulfide)				1	138

nd, not determined. Sulfide and thiosulfate values are averages of duplicate samples

than in the oxyHb sample and in the buffers. Both Hb^+ and oxyHb produced SHb of A_{618}/A_{576} ratio about 1.0 (Fig. 5). Another hemolysate (oxyHb 2) run at room temperature with stirring for 24 h resulted in a buffer bath with sulfide reduced from 800 to $15 \mu\text{mol} \cdot \text{l}^{-1}$, and in its place $530 \mu\text{mol thiosulfate} \cdot \text{l}^{-1}$ and $30 \mu\text{mol sulfite} \cdot \text{l}^{-1}$. The buffer in the tubing reached the same concentrations as the buffer bath, while the hemolysate in the tubing showed $15 \mu\text{mol sulfide} \cdot \text{l}^{-1}$ and $370 \mu\text{mol thiosulfate} \cdot \text{l}^{-1}$.

SHb remained stable through 24 h dialysis, with the A_{618}/A_{576} ratio remaining about 0.9 (Table 1, *bottom panel*). Other hemolysates ($30 \mu\text{mol heme} \cdot \text{l}^{-1}$) with SHb ratios of 0.89 and 0.94 (30 min after treatment with 1 and 5 mmol sulfide $\cdot \text{l}^{-1}$ in KCl-HEPES buffer) also retained SHb levels of 0.82 and 0.89 after 24 h dialysis in sulfide-free buffer (not shown in table). Green but turbid solutions usually resulted from the 24-h dialysis, presumably due to SHb plus elemental sulfur and some denatured protein. Sulfide-free hemolysates (control) in tubings remained bright red in the same dialysis buffer.

Effect of hemoglobin on sulfide oxidation

In the indirect assay of sulfide oxidation using BV and 5 mmol sulfide $\cdot \text{l}^{-1}$ no oxygen present, a positive linear relationship existed between nanomoles BV reduced or sulfide oxidized (y) and nanomoles heme (x) in killifish hemolysates: $y = 1.74 + 0.78x$, $r^2 = 0.83$ (data for 26 assays not shown; regression significant by ANOVA, $F = 117.74$, $P < 0.0005$).

However, the finding that hemoglobin was responsible for sulfide oxidation in the BV assays was not corroborated by the direct time-series assays with ^{35}S -sulfide. Killifish and mudsucker hemolysates incubated with $10\text{--}500 \mu\text{mol } ^{35}\text{S}\text{-sulfide} \cdot \text{l}^{-1}$ in oxygenated buffer of pH 7.4 showed little oxidation to thiosulfate. Figure 6 shows some of the time-series assays, comparing two different initial sulfide concentrations (*panels A and B*), ferrous oxyHb and ferric Hb $^{+}$ (*panels B and C*), and killifish and mudsucker (*panels A and D*). Sulfide concentrations decrease with time, faster at 140 than at $40 \mu\text{mol}$ initial sulfide $\cdot \text{l}^{-1}$, faster in the presence of Hb $^{+}$ than oxyHb, and at comparable rates in the two species under similar conditions. Sulfide disappearance was generally not matched by the appearance of stoichiometric amounts of soluble product(s), except in the presence of Hb $^{+}$ where thiosulfate was produced (*panel C*).

The rates for killifish obtained from 22 assays using oxyHb, 7 assays using Hb $^{+}$, and 12 control assays without hemoglobin are plotted against initial sulfide concentrations in Fig. 7A–C. Sulfide disappearance rates increased with initial sulfide concentration, and linear regression provided the best fit to the kinetics plots in the range of sulfide concentrations considered. The parameter estimates are summarized in Table 2; all individual regression coefficients are significant except for the thiosulfate rates in buffer. Significant differences were found between oxyHb and Hb $^{+}$ in the regressions for both

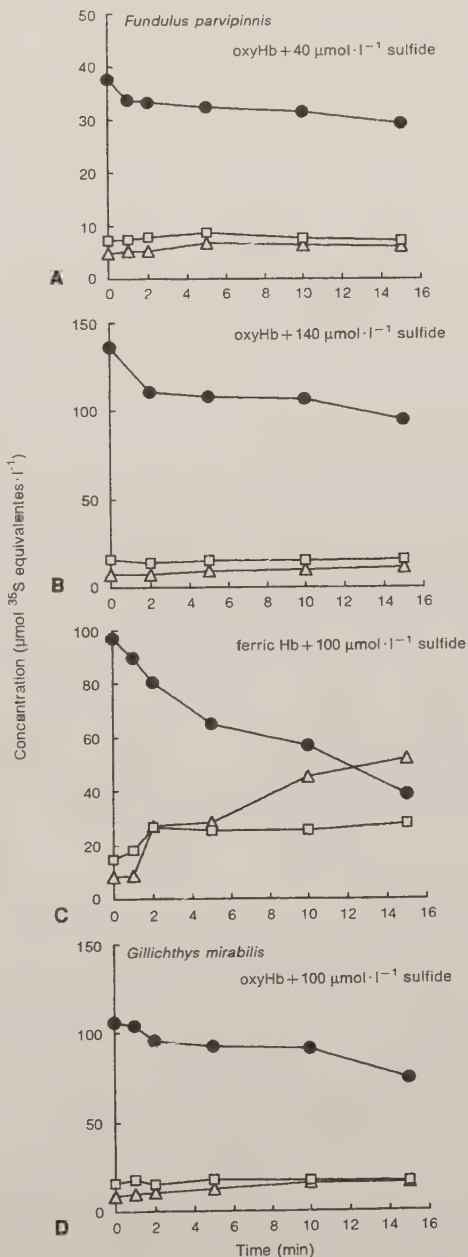


Fig. 6A–D. Changes in the concentrations of ^{35}S -sulfide (circles) incubated with red blood cell hemolysates. Thiosulfate (triangles) and sulfate (squares) present at time zero as contaminant in the ^{35}S -sulfide stock solution. A and B California killifish oxyhemoglobin ($293 \mu\text{mol heme} \cdot \text{l}^{-1}$). C California killifish ferric hemoglobin ($30 \mu\text{mol heme} \cdot \text{l}^{-1}$). D Long-jawed mudsucker oxyhemoglobin ($300 \mu\text{mol heme} \cdot \text{l}^{-1}$). ^{35}S was calculated as the $\mu\text{mol} \cdot \text{l}^{-1}$ equivalents from chromatographic peak areas of $200 \mu\text{mol sulfide} \cdot \text{l}^{-1}$ standards analyzed by bimeane-HPLC. Regression lines were fitted

to these four graphs and others to calculate the slopes = rates of sulfide disappearance and rates of product formation. For control rates in buffer only, refer to Figure 7

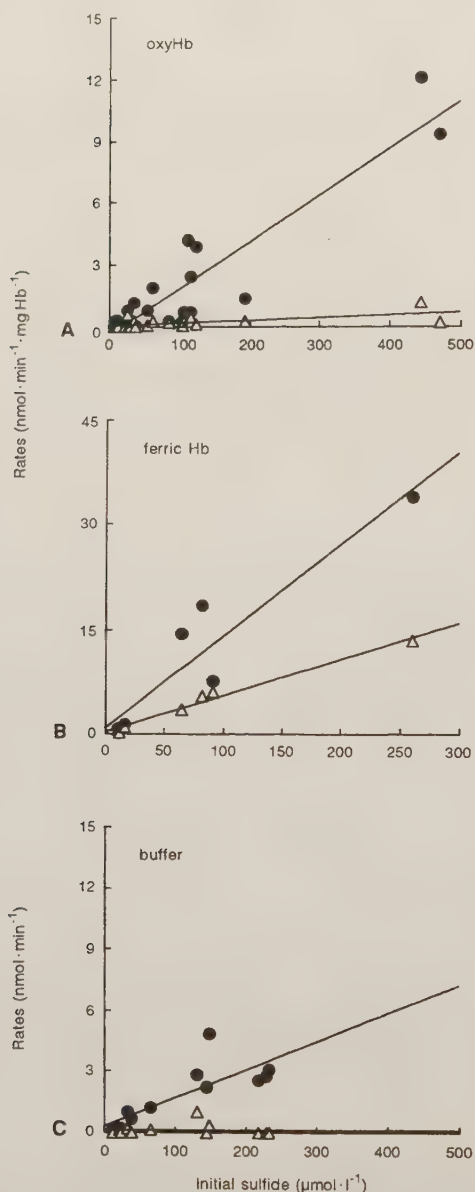


Fig. 7A–C. Kinetics plots of the rates of sulfide disappearance (circles) and thiosulfate formation (triangles) against initial sulfide concentration for California killifish ferrous oxyhemoglobin (A) and ferric hemoglobin (B). Rates in A and B normalized to hemoglobin concentration; note that ordinate scale of B is $3 \times$ that of A. C Control rates in buffer only. For parameter estimates of the regression equations, refer to Table 2

sulfide disappearance rates (Student's test, $t=9.28$, $P<0.001$) and thiosulfate formation rates ($t=28.09$, $P<0.001$). The rates in buffer were of slightly different units and not directly comparable to those in oxyHb and Hb^+ (normalized to milligrams Hb). Nevertheless, when the regressions for sulfide disappearance rates were tested together, oxyHb was different from Hb^+ but not from buffer, and Hb^+ was different from buffer (ANOVA, $F=60.65$, and Tukey's test, q values of $P<0.0005$). Sulfide disappeared at rates greater in the presence of oxyHb than in buffer alone, and even higher with Hb^+ . The regression of thiosulfate formation rates against initial sulfide concentration was deemed significant in oxyHb; however, the actual rates were low, particularly in comparison with Hb^+ (Table 2, predicted values).

Assays using whole blood showed a sulfide disappearance rate of about $2 \text{ nmol} \cdot \text{min}^{-1} \cdot \text{mg Hb}^{-1}$ at $3 \text{ mmol sulfide} \cdot \text{l}^{-1}$, lower than expected from extrapolation of the regression equations in Fig. 7A. This result suggested that the kinetics plot reached an asymptote at higher than $500 \mu\text{mol}$ initial sulfide $\cdot \text{l}^{-1}$, but no further study was made because of the difficulty of extracting enough whole blood.

Discussion

Sulfide-hemoglobin interactions have attracted a great deal of study, as the extensive literature cited indicates, and raised considerable confusion. To appreciate the multiplicity of hemoglobin-sulfide interactions it is important to realize that hemoglobin (and myoglobin) can participate in both ionic and covalent interactions with various molecules including sulfide. Coordination of the heme Fe, either ferric or ferrous, with ligands is an ionic interaction. For example, ferrous heme ligates O_2 and CO, but not sulfide; ferric heme ligates sulfide or cyanide, but not O_2 . "Methemoglobin" is ferric hemoglobin with a ligated water molecule. When ferric hemoglobin ligates sulfide, "sulfmethemoglobin" is formed. Ferric derivatives can be reduced to the ferrous form by dithionite. On the other hand, nucleophiles can potentially attack any double bond in the heme or in the protein and be covalently bound; this is what sulfide does in SHb formation. SHb is a bright green derivative with sulfur atoms covalently bound to the porphyrin as an episulfide, and with the heme either ferrous or ferric and capable of ligating various compounds. Ferrous SHb reversibly binds O_2 and CO but with different properties and kinetics than ferrous hemoglobin (Marchant et al. 1974; Carrico et al. 1978b; Brittain 1981). Ferrous SHb treated with ferricyanide produces ferric SHb that can bind the same ligands as ferric hemoglobin (Dijkhuizen et al. 1977; Brittain et al. 1982).

Sulfhemoglobin formation

Fish and mammalian hemoglobins share many similarities in spectral and physico-chemical properties (Riggs 1970). The present study on the California killifish and

Table 2. Parameter estimates of the linear regression: $y = a + bx$ of sulfide disappearance rates (y_1 , nmol sulfide $\cdot$ min $^{-1}$ $\cdot$ mg Hb $^{-1}$ in A and B, nmol sulfide $\cdot$ min $^{-1}$ in C) and thiosulfate formation rates (y_2 , nmol thiosulfate $\cdot$ min $^{-1}$ $\cdot$ mg Hb $^{-1}$ in A and B, nmol

thiosulfate $\cdot$ min $^{-1}$ in C) against initial sulfide concentration (x , μ mol $\cdot$ l $^{-1}$) in Fig. 7, including some predicted values of y for selected values of x

Assay medium/ regression	Parameters of regression				Predicted values of y for x equals			
	a	b	r^2	F statistic	20	50	100	250
A: With oxyHb ($n=22$ assays)								
y_1	-0.41	0.023	0.85	111.43**	0.44	0.73	1.86	5.34
y_2	0.08	0.001	0.38	12.11**	0.11	0.15	0.21	0.40
B: With Hb $^+$ ($n=7$ assays)								
y_1	0.94	0.131	0.88	36.90**	3.56	7.49	14.05	33.71
y_2	0.34	0.052	0.98	257.76**	1.38	2.94	5.54	13.34
C: Buffer control ($n=12$ assays)								
y_1	0.33	0.014	0.64	17.85**	0.60	1.02	1.71	3.77
y_2	0.16	0.000	0	0				

ANOVA of the regression coefficient, b , gives the F statistic; ** indicates $P < 0.0025$; r^2 is the coefficient of determination

other marine fishes shows that the formation of SHb is one of these similarities. Both the in vivo and the in vitro experiments show that fish hemoglobin is relatively insensitive to sulfide. The hemoglobin remains oxygenated in the presence of 20–100 μ mol sulfide $\cdot$ l $^{-1}$ (environmentally relevant for the killifish) and even high concentrations up to 1 mmol $\cdot$ l $^{-1}$. Only with 1 mmol sulfide $\cdot$ l $^{-1}$ and greater is SHb formed within a reasonable time frame (minutes to hours). Time, pH, heme concentration and ionic strength also affect the amount of SHb formed. The covalently bound sulfur does not come off even after 24 h dialysis of fish SHb, consistent with the conclusion of Carrico et al. (1978b) that SHb is an irreversible derivative. Since SHb rarely occurs in the blood of fish exposed to and killed by sulfide, the present study is in agreement with the conclusion that SHb is not a significant factor in cases of sulfide poisoning (National Research Council 1979). Sulfhemoglobinemia in humans is more often induced by drugs such as phenacetin than by H₂S inhalation (Park and Nagel 1984; Curry and Gerkin 1987). For animals in very high sulfide concentrations, SHb is a two-edged sword. Binding of sulfide as SHb can potentially ameliorate toxicity by removing some free sulfide from solution. However, SHb is practically non-functional in O₂ transport (Carrico et al. 1978b), and O₂ is necessary for sulfide detoxication by mitochondria (Bagarinao and Vetter 1990).

The green hemoglobin derivative was first observed and described as *Schwefelmethaemoglobin* by Hoppe-Seyler (1863), and later designated as *sulfhemoglobin* by Harnack (1898–99). Keilin (1933) generated sulfmethemoglobin from methemoglobin and sulfide, and showed it to be distinct from SHb. SHb has since then been produced and studied in vitro (Drabkin and Austin 1935–36; Evelyn and Malloy 1938; Michel 1938; Van Assendelft 1970; Carrico et al. 1978a, b; Brittain 1981; Brittain et al. 1982; Park and Nagel 1984; Park et al. 1986). Morell et al. (1967), Nichol et al. (1968) and Berzofsky et al. (1972) proposed similar reaction sequences for the generation of SHb and sulfmyoglobin

and showed that one mole porphyrin binds one mole sulfide. The National Research Council (1979) discounted SHb as a real chemical entity, and several other workers did not find SHb during exposure of animals or blood to sulfide. The present study has shown that SHb formation is strongly concentration, time, and pH dependent. Thus, previous reports of non-formation of SHb in marine worms may have been due to the low sulfide concentrations used: low micromolar sulfide (concentration not specified) in *Arenicola* (Patel and Spencer 1963a, b), 40–100 μ mol sulfide $\cdot$ l $^{-1}$ in *Riftia* (Arp et al. 1985), and 417 μ mol sulfide $\cdot$ l $^{-1}$ in *Abarenicola* (Wells and Pankhurst 1980). The hemoglobins of all these phylogenetically and ecologically diverse groups are probably not fundamentally different in their ability to bind sulfide in the porphyrin ring, but they do so significantly only at high sulfide, at low pH, and given enough time.

Hemoglobin in sulfide detoxication

The results of the present study disproves the notion that fish blood oxidizes sulfide to a significant extent and acts as the first line of defense to protect internal tissues (Bagarinao and Vetter 1989). The time-series assays and bimane-HPLC analyses show that killifish oxyHb or whole blood incubated with 10–500 μ mol sulfide $\cdot$ l $^{-1}$ do not produce much thiosulfate nor any other soluble product. Thus, the high thiosulfate concentrations in the blood of sulfide-exposed fish (Bagarinao and Vetter 1989) can not be due to hemoglobin-catalyzed sulfide oxidation. Sulfide disappears from oxyHb solutions probably because of binding to hemoglobin and oxidation to elemental sulfur. However, both processes occur at rates too low to be meaningful in sulfide tolerance. In the presence of oxyHb, sulfide disappears at 0.4 nmol $\cdot$ min $^{-1}$ $\cdot$ mg Hb $^{-1}$ in 20 μ mol sulfide $\cdot$ l $^{-1}$ and 5 nmol $\cdot$ min $^{-1}$ $\cdot$ mg Hb $^{-1}$ in 250 μ mol sulfide $\cdot$ l $^{-1}$ (Table 2). In contrast, mitochondria oxidize sulfide to thiosulfate at

maximal rate of $20 \text{ nmol sulfide} \cdot \text{min}^{-1} \cdot \text{mg protein}^{-1}$ in the presence of $20 \text{ } \mu\text{mol sulfide} \cdot \text{l}^{-1}$ and at half-maximal rate in $50 \text{ } \mu\text{mol sulfide} \cdot \text{l}^{-1}$ (Bagarinao and Vetter 1990). In terms of removal kinetics, oxyHb has low affinity for sulfide and moderate capacity that extends into relatively high sulfide concentrations (i.e., the rates increase with no "saturation" between 10 and $500 \text{ } \mu\text{mol sulfide} \cdot \text{l}^{-1}$, Fig. 7), whereas mitochondria have high affinity for sulfide and relatively high capacity that diminishes very rapidly at sulfide concentrations between 50 and $100 \text{ } \mu\text{mol} \cdot \text{l}^{-1}$ (Bagarinao and Vetter 1990).

Ferric hemoglobin is a better catalyst of sulfide oxidation. In the presence of Hb^+ , sulfide is oxidized to thiosulfate at maximal rate of about $34 \text{ nmol} \cdot \text{min}^{-1} \cdot \text{mg Hb}^{-1}$ in $250 \text{ } \mu\text{mol sulfide} \cdot \text{l}^{-1}$. However, the contribution of Hb^+ to sulfide detoxication is probably small since there is normally only about 1% Hb^+ in circulation (Jaffe 1981). Hb^+ was not detectable in California killifish in sulfide-exposure tests nor the controls; neither was it generated in vitro when sulfide was added to oxyHb. Catalysis of sulfide oxidation by Hb^+ has been suggested by Beck et al. (1981) to be more important than Hb^+S complex formation. In the killifish, Hb^+S was unstable (Fig. 4).

The results of the BV assays on killifish hemolysates were not corroborated by the results of radiolabeling experiments. While it seems certain that electrons are transferred to BV in the presence of sulfide and hemoglobin, it is not clear that the electrons come from sulfide. Perhaps electrons are released from hemoglobin when sulfide binds to the porphyrin ring, and BV reduction is a measure of sulfide binding rather than oxidation. Whatever the mechanism is, the conditions of the BV assay are highly unrealistic, and the purported sulfide-oxidizing activities mediated by BV [widely distributed among animals: Powell and Somero (1985, 1986b); Vetter et al. (1987); Bagarinao and Vetter (1989); Powell and Arp (1989); Vismann (1990)] probably have no in vivo physiological significance. Hematin (ferric heme not associated with protein) is the effective agent in some invertebrates (Powell and Arp 1989). Ferritin (non-heme protein that binds ferric iron) possibly contributes to sulfide-oxidizing activity with BV since it has been shown to catalyze sulfide oxidation in rats (Baxter and Van Reen 1958b).

Conclusions

Impairment of O_2 transport through SHb formation is not involved in acute sulfide poisoning of the California killifish and the long-jawed mudsucker. The high thiosulfate concentrations in the blood of sulfide-exposed fishes (Bagarinao and Vetter 1989) is not due to sulfide oxidation by hemoglobin. Oxyhemoglobin does not oxidize sulfide to thiosulfate at significant rates but covalently binds sulfide as SHb at high sulfide concentrations. Ferric hemoglobin forms an unstable ligand complex with sulfide and eventually oxidizes sulfide to thiosulfate, but this mechanism is probably insignificant in vivo. Thus,

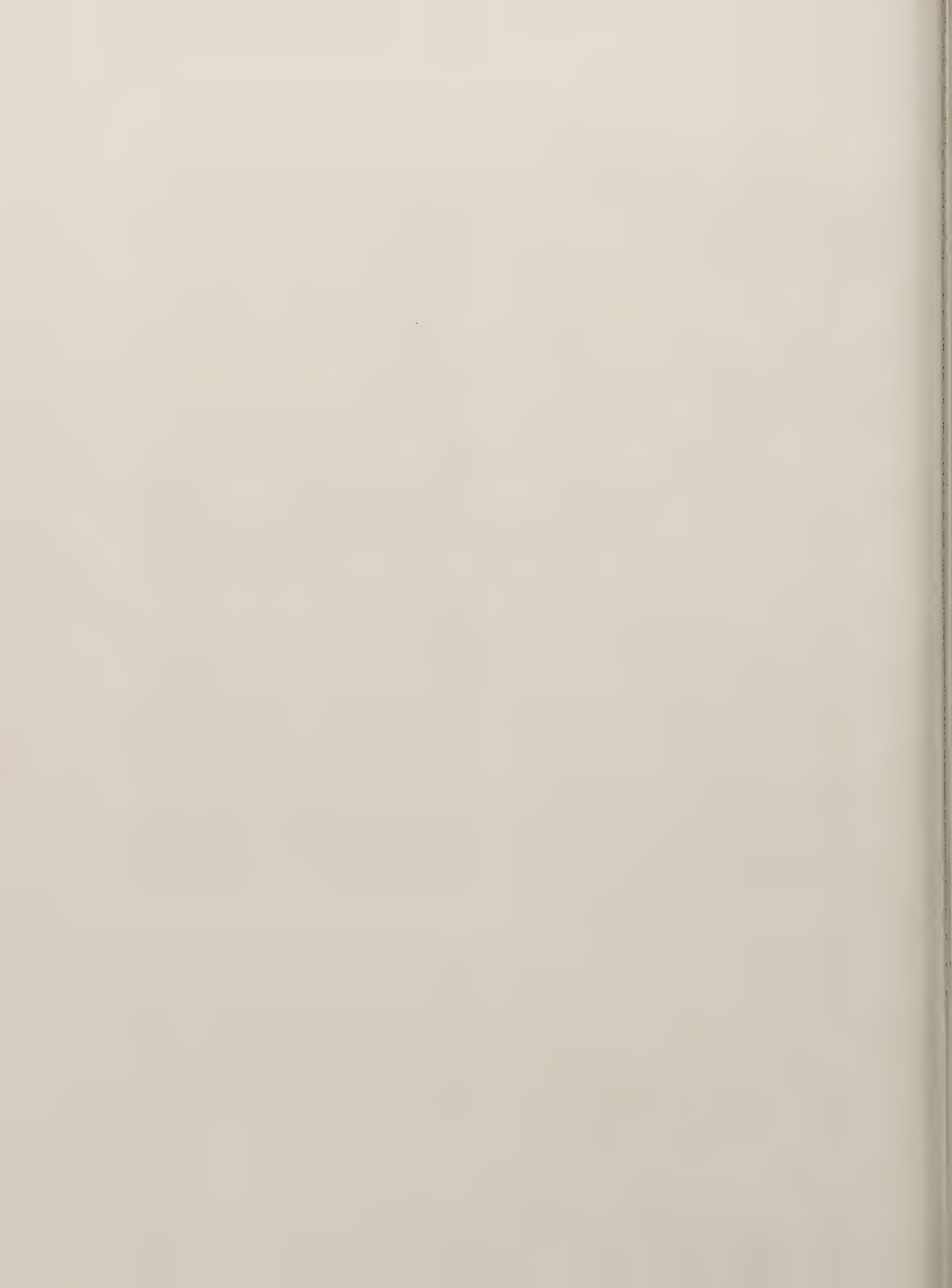
the blood only acts as depot for thiosulfate formed elsewhere in the tissues, probably by mitochondria (Bagarinao and Vetter 1990). Future studies on the interactions of heme proteins and sulfide must clearly differentiate between binding of sulfide and catalysis of sulfide oxidation. Additionally, they must show that the assay conditions, concentrations and products formed are consistent with data from whole-animal (natural and experimental) exposures.

Acknowledgements. T. Bagarinao thanks the SEAFDEC Aquaculture Department, the Fulbright Foundation and the Biology Department of the University of California, San Diego, for financial support. This research was supported by the National Science Foundation grant OCE-86-10513 to George Somero and RDV, Office of Naval Research contract N00014-88-0012 to RDV, and University of California Toxic Substances Research grant 504211-19909 to RDV.

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FISHBYTE SECTION

Editorial

This issue of *Fishbyte-in-Naga* has two papers on the inland fisheries resources of Bangladesh, and their relationship is obvious: any sound management policy rests on knowledge of the key features of the stocks that are exploited. These two papers thus document, for Bangladesh, how research and management may be articulated.

The relationship between the two papers on research on upwelling systems (to which charitable souls may add my essay in this issue of *Naga* on the "Peruvian anchoveta, Charles Darwin and us"), and the three papers on Lake Kariba may not be so obvious. There is a strong link, however: Lake Kariba, an artificial lake, was stocked with a clupeid *Limnothrissa miodon* very similar to the anchovies of upwelling systems, and the methods used or suggested

to study the now important *L. miodon* fisheries of Lake Kariba, are those traditionally used to study upwelling fisheries. Having established this link, I hope that researchers working on both types of systems will cooperate. *Fishbyte* can serve as a forum for these exchanges.

Mr. T. Sudjastani, whose obituary appears on p. 44-45, was also a friend of mine.

One more item: this issue of *Fishbyte* will be the last to bear Ms. Abbie Cruz-Trinidad's name as NTFS secretary. She will be replaced in January 1993 by Ms. Beth Eleccion. I thank Abbie for many years of creative and respectful interactions (but wait: she is not gone. She will still contribute to *Fishbyte* as an author!). D. Pauly



The Climate and Eastern Ocean Systems Project

A. BAKUN, V. CHRISTENSEN, C. CURTIS, P. CURY,
M.H. DURAND, D. HUSBY, R. MENDELSSOHN,
J. MENDO, R. PARRISH, D. PAULY
and C. ROY

Abstract

A brief description of the NMFS/ORSTOM/ICLARM Climate and Eastern Ocean Systems (CEOS) project is given. CEOS will study the four major eastern boundary current regions (Peru/Chile, California, Northwest and Southwest Africa) and attempt to separate local short-term changes of their resources and/or dynamics from long-term, climatic global changes. Expected products range from a large, widely accessible oceanographic/atmospheric database to various documents that will present key results as well as improved contacts and stronger analytical capabilities in cooperating national institutions.

Introduction

The injection of millions of tonnes of greenhouse gases into the earth's atmosphere may be viewed as a gigantic experiment aimed at exploring the earth's reaction to such challenge. Unfortunately, this experiment is run without proper "controls", and hence the heated debates about the actual impact of those gases may last too long, beyond the time where the "experiment" should be called off. The international scientific community is forced, however, to address this problem in spite of the lack of scientific controls.

One way to address this is through the comparative method, a major tool in those disciplines in which experiments

are hard to perform, e.g., evolutionary biology (Mayr 1982), and fisheries science (Parrish et al. 1983; Bakun 1985).

Given the importance of the four major upwelling systems off Peru/Chile, California, Northwest and Southwest Africa (Fig. 1) both as sources of fish and as CO₂ "pumps", scientists from the Pacific Fisheries Environmental Group (PFEG), the National Marine Fisheries Service (NMFS), Institut Francais de Recherche Scientifique pour le Développement en Coopération (ORSTOM), and the International Center for Living Aquatic Resources Management (ICLARM), and partners from other institutions have teamed up to investigate these systems in the context of global changes, through a project called CEOS (Climate and Eastern Ocean Systems) funded by the National Oceanic and Atmospheric Administration (NOAA) and ORSTOM.

Objectives of CEOS

The CEOS project is an international collaborative study of potential effects of global climate change on the living resources of the highly productive eastern ocean upwelling ecosystems and on the ecological and economic



Fig. 1. Location of the four major upwelling systems to be investigated by CEOS, with photos of some of the major sources of information on these systems.

issues directly associated with such effects. A major focus of the study are the clupeoid fishes (anchovies, sardines, etc.) that are heavily exploited in these large marine ecosystems and which have recently been exhibiting episodes of collapse, rebound, or switches in dominance.

The major objectives of the CEOS project are thus to: 1) assemble, summarize, and analyze the data record of the past four decades regarding the four eastern ocean boundary upwelling ecosystems mentioned above along with data from other upwelling areas; 2) apply the comparative method to identify key physical processes and ecosystems responses; 3) resolve underlying global-scale trends in each individual regional system that may be obscured by local interyear and interdecadal variability; 4) investigate the relationship of these global trends to accumulating greenhouse effects; 5) construct scenarios for future consequences of global climate change on upwelling resources; and 6) analyze and project ecological and social impacts on associated human activities and values.

Eastern ocean upwelling ecosystems present certain advantages that may make the study of effects of climate change on marine ecosystems particularly tractable; thus the study may serve an even wider purpose as an illustration of the sorts of impact that could affect more complex marine ecosystems.

The most immediate response to greenhouse warming is expected to occur within the atmosphere rather than

within the ocean, affecting the wind field over the ocean, and hence, patterns of upwelling. Bakun (1990) presents evidence of this already occurring over the past decades. Thus global climate change could substantially alter the factors that determine favorable reproductive habitat, long before ocean temperature changes brought on by greenhouse warming may be evident.

By analyzing time series data from similarly functioning regional ecosystems distributed over the globe, we hope to tease out the significant global trends from within the "noise level" of naturally occurring regional climatic variability. By these, trends can be mechanistically linked to accumulating greenhouse effects, and would constitute one basis for projection into the future.

A somewhat independent basis for projecting effects of climate change will be sought in the analysis of the large amplitude natural regional variability (i.e., the "noise") overlying the trends. That is, ecosystem responses to shorter-period interyear variations in large-scale atmospheric forcing that may be confined to a single region will also be analyzed. In this approach, greatly increased degrees of freedom for empirical model formulation and verification are obtained from the more numerous realizations of shorter period events in the data record and from the fact that the different regional sets of realizations may be independent from one another.

Some initial scenarios are already available. For example, Bakun (1990) has argued that one consequence of increased greenhouse effects that can be confidently expected is that temperature gradient between the ocean and the continents will increase during the spring-summer upwelling seasons in these systems. This would be reflected in increased alongshore wind and enhanced sea breeze circulation, which would impact recruitment (Mendelssohn and Mendo 1987). Evidence exists for an "optimal environmental window" with respect to wind effects (Fig. 2), such that changes in characteristic wind speed may disrupt finely tuned reproductive strategies of the small pelagic fishes which are essential trophic components of these ecosystems.

Another approach to identifying trends in ecosystem processes will be through the construction of sequences of trophic models of the ecosystems and by computing

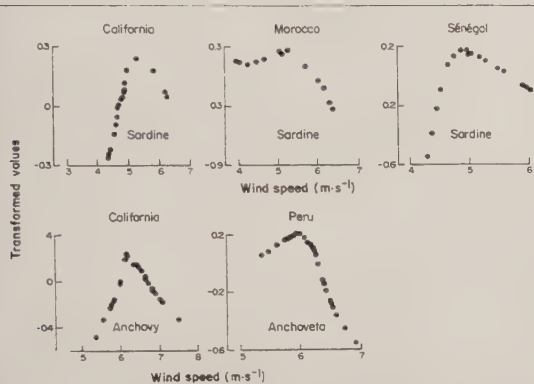


Fig. 2. Showing a general pattern extracted by comparative analysis of several upwelling systems: optimal recruitment occurs, in clupeoids, when wind speed is moderate (4-6 m.s^{-1}) and leads to moderate upwelling (adapted from Cury and Roy 1989, 1991, and unpublished data).

the values of indices expressing their emergent properties. Emphasis will be given to the theory of Ulanowicz (1986) and to the concepts of maturity, stability, and especially "ascendency", an emergent attribute of ecosystem models that encompasses their size as well as their structure. The ECOPATH II software of Christensen and Pauly (1992), a derivative of the ECOPATH program developed by J.J. Polovina and collaborators at the NMFS Honolulu Laboratory, will be used for construction of several

models for each of the investigated systems.

Identification of trends attributable to (global) climate change and of the mechanisms for change (or conversely, for homeostasis) will be attempted via detailed analysis of temporal changes in ascendancy and related indices. The analysis will include comparisons among upwelling systems and also comparisons with models of other systems (coral reefs, estuaries, freshwater bodies, etc.) presently being accumulated at ICLARM within the framework of a project on "Global Comparisons of Aquatic Ecosystems" (Christensen and Pauly, in press).

Human activities facing local and global changes are also studied. The exploitation of marine renewable resources in the different upwelling areas appears to be a real challenge due to the fact that these resources are unstable. Comparative analyses of market response to local and global changes will be studied - building up on contributions in Cury and Roy (1991), and Durand

et al. (1991) - in Peru, Morocco, and Sénégal. Also, detailed analysis of time series of fish meal exports and prices, i.e., of one of the main products from upwelling systems, will be performed.

This will give some new insights on how human activities are coping with economic and social change at different levels of organization, from which different new approaches on how to use unstable renewable resources may be derived.

Brainstorming Workshop on Simulation Modelling of the Peruvian Upwelling Ecosystem

ASTRID JARRE-TEICHMANN
WOLF HERTLEIN
S.E. JØRGENSEN

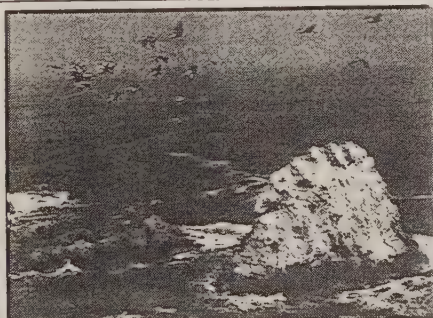


Fig. 1. Pelicans off the Peruvian coast—their much reduced populations reflect the much reduced populations of anchoveta, their main prey. (Photo by A. Jarre-Teichmann).

Faithful readers of *Naga* will note that Fig. 1 is a reproduction of the cover photo of the April 1990 issue, which also included a brief remark on ICLARM's

collaborative research with the Instituto del Mar del Peru (IMARPE) at Callao, Peru, on the Peruvian upwelling ecosystem. This cooperation, aimed ultimately at a model for managing the large pelagic fisheries of Peru, resulted to date in the construction, (partial) analysis and

publication of a considerable database, including 30 years' worth of oceanographic and biological time series (see contributions in Pauly et al. 1989). Recent progress included the construction of a set of 17 trophic (ECOPATH II) models (Jarre-Teichmann 1992), including models of three periods characterized by different species dominance and fishing patterns systems, "monthly" models capturing seasonal changes and models typifying warm and cold temperature anomalies (El Niño/La Niña).

An informal workshop on "Simulation modelling of the Peruvian upwelling ecosystem" has recently been conducted with ICLARM support, in the context of the CEOS Project (see p. 26). Five scientists of the informal Danish "Copenhagen Modelling Group" (CMG), i.e., the last author, as well as Henning Mejer, Henrik Maler, Søren Nielsen and Jørgen Salomonsen met with AJT and WH at Kollekolle Seminar Center near Copenhagen during 19-20 August,

Linkages of the CEOS Project

The CEOS project addresses most of the strategic and integrating priorities listed in the U.S. "Global Research Program Priority Framework", especially the "Ecological Systems and Dynamics" category, and addresses in some way most of the issues listed under that category: e.g., "(assembly and analysis of) Long-Term Measurements of Structure/Function", "Response to Climate and Other Stresses", "Interactions Between Physical and Biological Processes", "Models of Interactions, Feedbacks, and Responses", "Productivity/Resource Models", etc.

The project is designed within the general framework of the International Program of Ocean Science in Relation to Living Resources (OSLR), which is cosponsored by the Intergovernmental Oceanographic Commission and the Food and Agriculture Organization of the United Nations (Bakun et al. 1982). It can be considered an initial effort in the newly proposed subprogram of OSLR and Ecosystem Dynamics and Living Resources (EDLR). Elements of CEOS directly related with "recruitment" constitute contributions to the Sardine-Anchovy Recruitment Project (SARP), a major component of the International Recruitment Program (IREP) of OSLR.

Several national research laboratories working on similar systems are associated with this project through a cooperative agreement with ORSTOM. This project presently includes: the Institut Scientifique des Pêches Maritimes, Morocco; the Centre de Recherches Océanographiques d'Abidjan, Côte d'Ivoire; the Fisheries Research Utilization Branch,

Ghana; and the Centre de Recherches Océanographiques de Dakar-Thiaroye, Sénégal, which will focus on regional case studies of climatic variability, coastal ecosystem dynamic and associated human responses. The collaboration of scientists from these institutes with the CEOS project is funded by the Scientific Committee on Dynamics and Use of Renewable Resources (DURR) of ORSTOM. Other national institutions are linked directly with the project, and/or through their own linkages with ICLARM.

Expected Products and Results of the CEOS Project

The project is expected to produce new insights - but these we cannot plan. We have planned some of the products, however, in which these insights will be presented. These will be:

- a multi-authored book, tentatively titled "Global versus Local Changes in Marine Pelagic Systems", which will contain most of the research results;
- one synopsis for each of the four anchovy species making up the bulk of the biomass in each of the abovementioned ecosystems (*Engraulis ringens*, *E. mordax*, *E. encrasicolus* and *E. capensis*);
- a report presenting ECOPATH II models of the four systems, and the data upon which they are based;
- various scientific papers in the primary literature.

1992, for a brainstorming session on the conceptualization and construction of a spatially structured simulation model of the system. The participants agreed that the model should be aimed at predicting sustainable anchoveta catch for a few months in the future, given coastal wind, temperature observations, and a fishing pattern. The model should consider the biological interactions among the key fish species anchoveta, sardine, mackerel, hake, and bonito, as well as the impact of the fishery on these groups. The model should also consider the pinnipeds and guano birds as additional top predator groups.

After construction of a conceptual diagram of the model inspired by earlier work of Dr. Peter Muck of the GTZ/IMARPE PROCOPA Project (Jarre et al. 1991), the participants agreed to proceed as follows:

- (i) Construction of single-species model of Peruvian anchoveta in an artificial environment, disregarding spatial resolution;

- (ii) Stepwise inclusion of the other four major fish groups into this model;

- (iii) Inclusion of spatial resolution, as required for fisheries management, with alongshore, offshore, and depth components.

The group also listed the required state variables, forcing functions and parameters, as well as the set of nonlinear differential equations that will be used for the construction of the anchoveta model, which is now being parameterized by WH and will be programmed and evaluated in direct cooperation with Jørgen Salomonsen within the next few months.

The model will include a user-friendly output interface based on the GEOMARPE software developed at ICLARM, thus enabling Peruvian scientists and fisheries managers to assess immediately the results of different model runs and, e.g., evaluate the consequence of alternative fishing patterns under given meteorological oceanographic conditions.

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A. JARRE-TEICHMANN and W. HERTLEIN are from Alfred Wegener Institute of Polar and Marine Research, Bremerhaven, Germany. **S.E. JØRGENSEN** is with the Royal Danish School of Pharmacy, Copenhagen, Denmark.

FISHBYTE SECTION

The CEOS project, as one of its contributions, will make the Comprehensive Ocean-Atmosphere Data Set (COADS) available for use on MS DOS and Mac II Personal Computers at two different levels of resolution.

Worldwide data on air temperature, sea-surface temperature, surface winds, sea-level pressure and number of observations were extracted for 1946-90 from the Word Weather Disk (CD ROM) and from original COADS files, then implemented into microcomputer files.

A program called CODE2 was then written which can be used at the first level of resolution to retrieve monthly means by 2° squares, pertaining to a single box or a complex staircase of 2° boxes along a coastline. Output from the CODE2 program consists of annual and monthly output files, and a binary file of the selected data. The annual output file shows on a single line the 12 monthly means of a single parameter for a year, by parameter. The monthly output file shows all five parameters for a year, by month. The data are comma delimited in each output file, allowing for easy import into spreadsheet and/or graphics software.

The second level of resolution will create programs for retrieving the raw data (rather than 2° monthly means) from the COADS data set. This involves more than 2.5 gigabytes of data, starting from 1870. Before this reorganization, access to the COADS data set was available only on a mainframe computer and was a slow and tedious process. Contact the CEOS Project, c/o PFEG for details.

Also, the project will support the entry into FISHBASE, a computerized encyclopedia of fish (Pauly and Froese 1991), of the biological data on the major fish species in each of the abovementioned four upwelling systems. Further, the CEOS project will make available, most probably on CD-ROM (laser) disk, the time series of oceanographic and other data upon which trend analyses will be based. This applies particularly to the COADS data set, which will be made available for use on MS DOS (and Macintosh) personal computers (box).

Timing and Additional Linkages

The PFEG and ORSTOM component of the CEOS project began mid-1991 when Claude Roy and Philippe Cury, both from ORSTOM, began what will be a two-year stay at PFEG, in Monterey, California, USA, while the two-year ICLARM component (D. Pauly and V. Christensen) began in September 1992.

Thus, the project will last until mid-1994 at least, and this offers numerous possibilities for interested colleagues in developing or developed countries to team up with us. If you are interested, please write to the CEOS project at PFEG, P.O. Box 831, Monterey, California, 93942, USA, or fax us at (408) 646-3319.

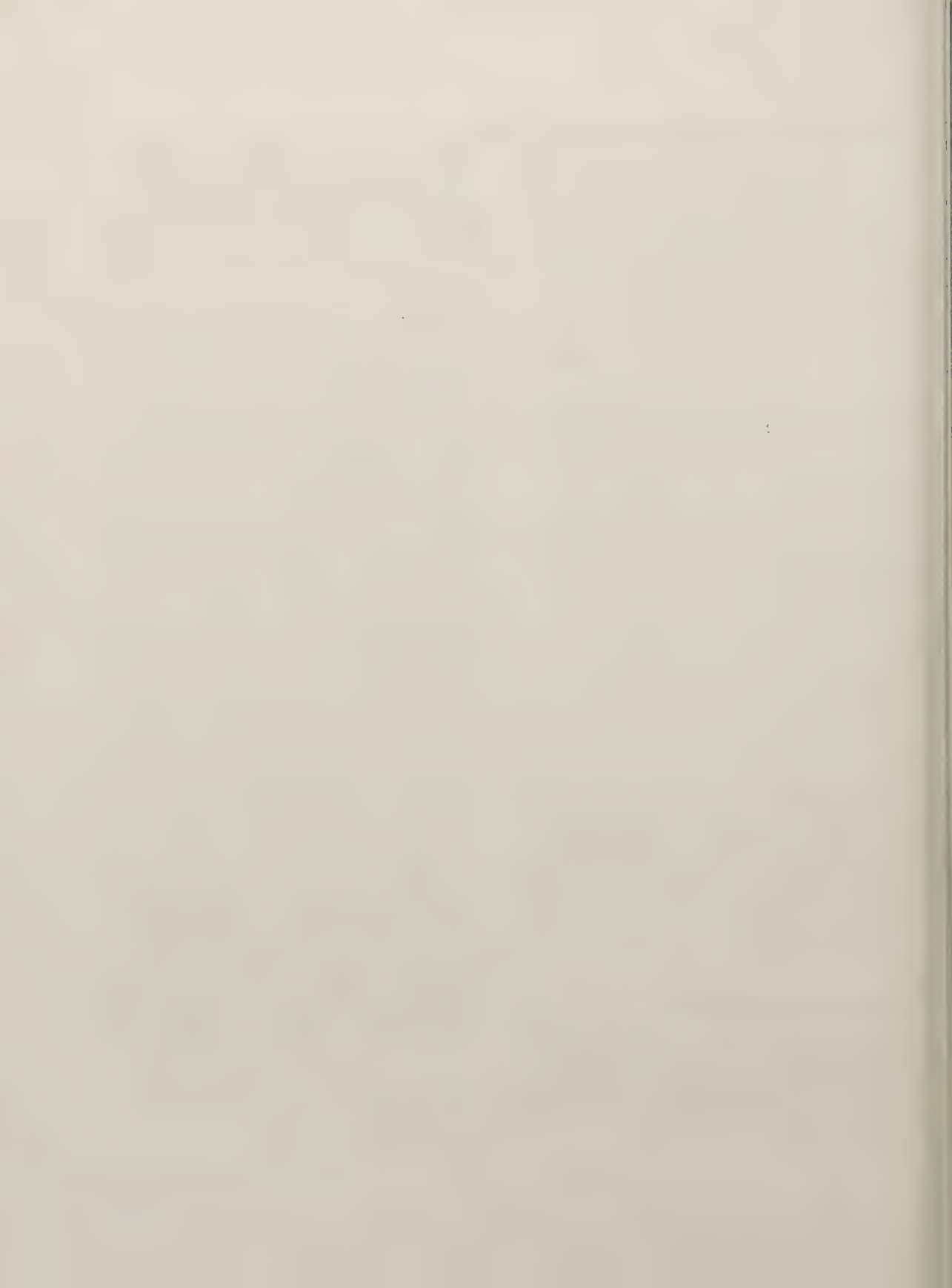


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HABITAT USE PATTERNS AND RANGES OF THE BOTTLENOSE DOLPHIN IN THE GULF OF CALIFORNIA, MEXICO

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ABSTRACT

I studied behavior and range patterns of individual bottlenose dolphins during 1984 in the mid-eastern Gulf of California, Mexico. Dolphin sighting rate was significantly higher in areas close to estuary mouths, 0.306 sightings per hour compared with 0.155 sightings per hour in areas distant from estuary mouths. Dolphins used these estuarine areas to feed; 61% of all behavior observed near estuaries was feeding as compared with 23% elsewhere. Traveling comprised 61% of all behavior observed in areas distant from estuary mouths. Estuaries are sites of large concentrations of nutrients which support great numbers of filter-feeding zooplankton and fish. Bottlenose dolphins may specialize on estuarine prey, or they may feed in estuarine areas simply because of the abundance of potential prey that these systems support. In either case, data on relative numbers, distribution patterns, behavior and diet indicate that this is a general trend in habitat use for many coastal populations of this species in the Pacific and Atlantic.

Ranges of a few individuals spanned a minimum of 65 km of coastline, and animals were not permanent residents of a monitored bay. In contrast, dolphins off the coast of Sarasota, Florida, have been reported to be year-round residents with smaller ranges. This difference in degree of site fidelity may be related to habitat differences. The west coast of Florida is dotted with numerous and large estuarine systems which may host permanent prey populations and support resident groups of dolphins. The Gulf of California coastline contains few estuaries; most are small and perhaps support prey resources which are ephemeral, requiring dolphins to range over larger distances in search of food.

Key words: bottlenose dolphin, *Tursiops truncatus*, behavior, habitat use, home range, photo-identification.

Habitats are generally composed of a mosaic of patches which differ from each other physically and biologically. Some patches offer more protection from the elements or from predation; others offer less. Some patches support large concentrations of food; others are barren. Because of such heterogeneity we

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expect to see specific patterns in the way animals are distributed and in the way they use patches within a given habitat.

This is the case for several species of cetaceans. Spinner dolphins (*Stenella longirostris*) in the Hawaiian islands rest in shallow, sandy areas in coves or atolls during the day and move into deep water to forage at night (Norris and Dohl 1980). Humpback dolphins (*Sousa* sp.) along the southeastern coast of South Africa feed among reefs along an unsheltered, rocky coastline, but rest, mate, play, and move within a sheltered bay with a sandy bottom (Saayman *et al.* 1972, Saayman and Tayler 1979). Killer whales (*Orcinus orca*) in Puget Sound feed over areas of high relief in bottom topography and travel across deep water areas with relatively little topographic relief (Heimlich-Boran 1987).

Habitat heterogeneity and the biological requirements of a species interact not only to produce these patterns in distribution and in habitat use, but also to influence the size of an animal's home range (McNab 1963). Specifically, the body size and energy requirements of an animal dictate the amount of energy necessary to maintain this individual. The abundance, distribution and availability of resources within the habitat determines the size of an area which will fulfill these energy requirements. The result of the interactions between these factors is manifested in the size of the home range.

These factors, distribution, habitat use patterns and home range size, are intricately related to features of an animal's habitat. In this paper, I document distribution, habitat use patterns, and range of bottlenose dolphins (*Tursiops truncatus*) in the Gulf of California, Mexico. I then compare these characteristics to a population of bottlenose dolphins off the west coast of Florida and conclude that specific habitat features may influence ranging behavior of this species.

METHODS

Research was conducted during the spring, summer, and fall of 1984, along the west coast of mainland Mexico in the Gulf of California (Fig. 1). I surveyed 200 km of coastline and waters around mid-gulf islands at a constant speed of five knots from one of two boats: a 3.6-m, 165-hp inboard-outboard Sterncraft or a 10-m, twin 155-hp Skipjack during 562.2 h. Of these, 186 h were spent in direct observation of bottlenose dolphins. Prior to this, a pilot study was conducted during the summer of 1983. None of the 1983 preliminary data are included in the present analyses.

Once a group was sighted, I followed and observed dolphins from a distance of 50 m or more for periods of 30 min to 6 h. During this time, I continuously recorded location, movements, and number of individuals in the group. I monitored weather, sea conditions, water depth, water temperature, and secchi disc depths each 15 min.

I also monitored activity patterns. Groups habituated to the boat and resumed their normal activity within half an hour after observations began. Accordingly, I continuously recorded the behavioral state of dolphins from 30 min after the initial sighting of the group until the end of the observation period for that group. All individuals in a group exhibited the same general behavioral state;

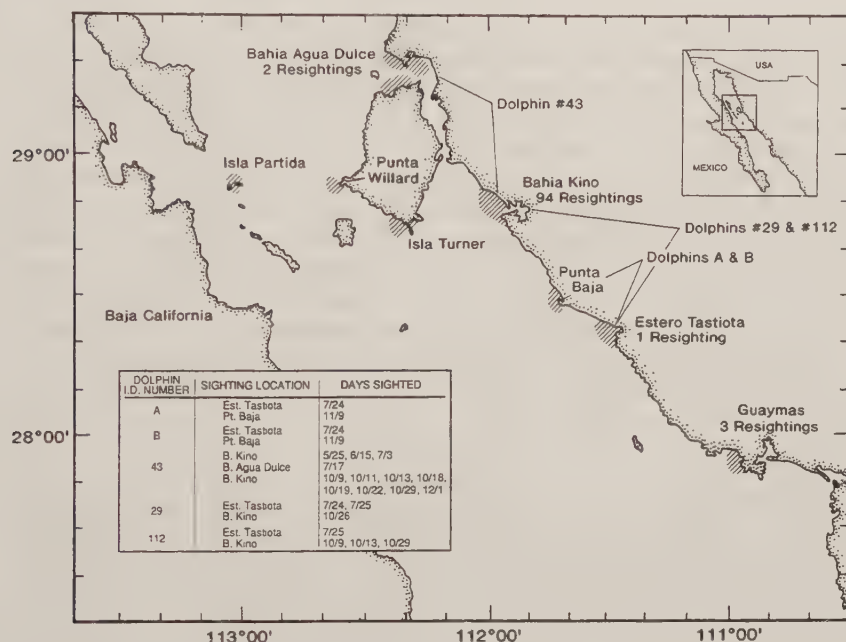


Figure 1. Map of the study area, the mid-eastern Gulf of California, and sighting locations of dolphin groups, indicated by shaded areas. The number of individuals resighted in each area and location of animals sighted in more than one area are indicated. The inset gives location and date of sightings of animals photographed in more than one area.

the behavior patterns I recorded represented the activity of each group as a unit. I classified activity into one of several categories which are described below. I did not quantify discrete behaviors such as leaps, spy hops, tail slaps and vocalizations.

The dorsal fins of *Tursiops* are regularly nicked and scarred, and these markings are unique features which can be used to identify individuals (Würsig and Würsig 1977, Ballance 1990). In order to monitor the movements and associations of individual animals, I attempted to photograph the dorsal fin of each animal in all groups. I used an Olympus camera with a motor drive and data back, a 200-mm lens and Kodachrome (K-64) color slide film. I took over 7,000 photographs during the study. In the laboratory, I identified individuals from these photographs by viewing the slides under a dissecting microscope.

The 200 km of coastline I surveyed included a variety of habitats ranging from shallow, turbid waters with sandy bottoms to rocky shores dropping abruptly to deep depths in clear water. I assessed the distribution and behavior patterns of *Tursiops* for two habitat types: estuarine and non-estuarine. I arbitrarily chose three nautical miles (5.5 km) to define the boundary between these two habitat types: waters within three nautical miles of the mouth of an estuary

were labeled estuarine and waters farther than three nautical miles were labeled non-estuarine. Habitat use was compared by calculating the number of sightings of dolphin groups in a particular habitat divided by the number of hours spent surveying this habitat.

I quantified ranges by analyzing photographs of individuals from the entire study area and calculating distances between areas in which the same animal was sighted. I use the term "range" simply to denote that area within which an animal has been sighted. This is distinct from "home range" which is defined as the area over which an animal normally travels in pursuit of its routine activities (Burt 1943). Conclusions about an animal's home range may be made only after details about daily and seasonal movements and activities are known. Results of this study comprise a series of sightings of individual animals; these sightings outline only a portion of the home range of these individuals.

RESULTS

Behavior—Behavior of bottlenose dolphins could readily be classified into four categories which I have termed feeding, traveling, resting, and socializing.

Feeding was characterized by no directional movement. Animals generally surfaced and dove asynchronously while the entire group remained loosely aggregated over an area of several hectares. Occasionally, an individual would pursue prey at the surface by swimming upside down at high speed with pectoral fins in the air. These animals were apparently feeding individually. On a few occasions, animals appeared to feed cooperatively, surfacing synchronously in a large circle, then diving in toward the center. Tightly grouped balls of bait fish were sometimes visible beneath the surface in the center of the area where the dolphins dove. I directly witnessed prey capture by dolphins on a few occasions, when dolphins were exhibiting each of the above behaviors.

Seabirds were frequently present with feeding groups of dolphins. Brown pelicans (*Pelecanus occidentalis*), blue-footed and brown boobies (*Sula neubouxi* and *leucogaster*), double-crested cormorants (*Phalacrocorax auritus*), and magnificent frigatebirds (*Fregata magnificens*) were the most common species associated with these feeding groups. Flocks of these seabirds, circling and diving, were so indicative of feeding dolphins that this became one of the most reliable methods of locating a group and classifying feeding behavior.

Traveling was characterized by directional movement of a group. Traveling animals moved as a unit, diving and surfacing synchronously at speeds of three to five knots. Dives averaged two and one-half to three minutes and surface intervals consisted of several respirations during a time interval of approximately 30 sec.

Resting was characterized by low levels of activity during which almost no forward movement of animals occurred. A resting animal slowly rose to the surface with its head and dorsal fin breaking the water simultaneously, remained afloat for up to 10 sec, and slowly submerged again with almost no forward rolling motion.

Socializing was characterized by a high level of activity. Socializing animals surfaced together in a tight aggregation and often remained at the surface for several minutes. During this time, animals exhibited prolonged body contact and furious activity. Body contact often took the form of slaps of the flukes or pectoral fins of one animal against the body of a second.

Traveling and feeding occasionally occurred simultaneously with animals moving along a coastline, stopping to feed, and resuming travel once more. Traveling also occurred in conjunction with socializing. No other combination of two or more behaviors was observed.

Habitat use patterns—I observed 93 groups of bottlenose dolphins during the study. These groups were not dispersed evenly over the entire study area. Dolphins were generally sighted in shallow, turbid water where the bottom was composed of sand. Dolphins also remained close to the coast. Only three groups moved farther than five km from shore, and the majority were observed within three km from shore. Water near rocky coastlines, water over 10 m deep and clear water were areas of few dolphin sightings.

Dolphin sighting rate and number of schools were highest in areas near the mouths of estuaries (Table 1). Twice as many groups per hour were sighted in areas within 5.5 km from the nearest estuary mouth as compared with areas farther than 5.5 km from the nearest estuary mouth. This difference in sightings per hour was significant ($\chi^2 = 8.33$; $P < 0.05$).

Dolphins used these habitats near estuary mouths to feed (Fig. 2). Sixty-one percent of all behavior observed in areas within 5.5 km of an estuary mouth was feeding. The next most prevalent behavior was traveling, comprising 22% of the behavior in these areas. In areas farther than 5.5 km from an estuary mouth behavior was strikingly different. Sixty-one percent of all behavior observed here was traveling; 23% was feeding. Resting and socializing comprised approximately the same percentage of the behaviors observed in both locations.

Ranges—Ninety-three dolphin groups were sighted in eight separate locations (Table 2). The vast majority of these were sighted in Bahia Kino, as expected from the high number of survey days in this area. The number of groups sighted in the seven areas outside of Kino is low because of the small number of survey days in these areas.

Two hundred six individual dolphins were identified during the study. Of these, 155 were sighted in Bahia Kino and 51 were sighted in seven additional locations along the coast to the north and south of Bahia Kino and around several offshore islands (Fig. 1 and Table 2).

The 155 individuals identified in Bahia Kino represented a majority of the animals visiting this bay during the study period (Ballance 1990). Seventy individuals were identified during the first month of the study, from mid-May to mid-June. Another 75 were identified during the last three weeks of October. But during the months of November and December, only five previously unidentified individuals were photographed in Bahia Kino. This means that these animals could be recognized if they traveled to other locations within the study area.

Many individuals were sighted in the same location more than once (Fig. 1).

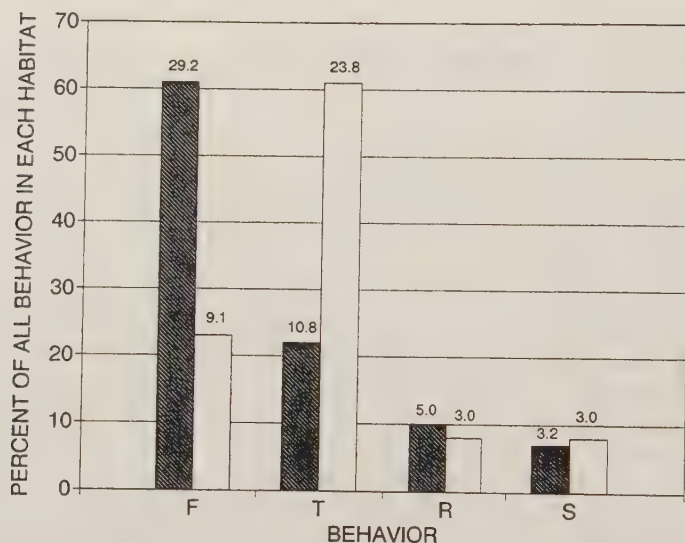


Figure 2. Behavior of bottlenose dolphins in two habitat types: areas near and far from estuaries. Light-colored bars indicate behaviors observed in waters farther than 5.5 km from an estuary mouth; dark-colored bars indicate behaviors observed in water closer than 5.5 km from an estuary mouth. Letter abbreviations represent behavior categories: F = feeding, T = traveling, R = resting, S = socializing. Numbers above each column represent hours of observation of each behavior category.

Ninety-four of the 155 individuals identified in Bahia Kino were sighted there between two and 11 times (Ballance 1990). Three of the seven animals identified in Guaymas were sighted there twice: two animals on 7 and 8 July and one animal on 11 and 12 November. One of the 16 animals identified in Estero Tastiota was sighted there twice, on 24 and 25 July. Two of the 12 dolphins identified in Bahia Agua Dulce were seen there twice, both animals on 17 and 18 July. All of the animals resighted in the areas outside of Bahia Kino and many of those resighted in Bahia Kino were sighted on adjacent days.

Of the 206 individuals identified throughout the study area, only five were seen at more than one location (Fig. 1). The distance between sightings for these individuals varied from 25 to 65 km.

DISCUSSION

It is widely believed that a single species of bottlenose dolphin is cosmopolitan and exhibits a series of forms which differ behaviorally and morphologically (Leatherwood and Reeves 1983a). Results of this study pertain only to the inshore, coastal form, although both inshore and offshore morphs have been reported in the Gulf of California (Walker 1981).

Behavior—Bottlenose dolphin behavior is generally described in terms of four major categories: feeding, traveling, social interactions, and idling (Shane *et al.*

Table 1. Bottlenose dolphin presence in two habitat types, areas near and far from estuaries. Group sighting rate was significantly higher in areas close to an estuary mouth.

Distance to estuary mouth	Survey effort (hours)	Dolphin groups sighted	Sightings per hour
<5.5 km	228.5	70	0.306
>5.5 km	148.0	23	0.155

1986), and the dolphins in this study exhibited behavioral patterns which clearly fell into these four groups.

Feeding is a particularly interesting behavior because of the diversity of specific techniques that have been documented for this single species (reviews by Leatherwood 1975, Shane *et al.* 1986, Shane 1990b). In Bahia Kino feeding individually, presumably on dispersed prey items, was the predominant strategy. I also observed a few instances of apparent cooperation between the individuals of a group.

Shrimp boats operated in the area during approximately one-half of the study and were often trawling or hauling in nets within a few km of a dolphin group. In the Gulf of Mexico dolphins frequently feed behind working shrimp boats during all stages of the fishing operation (Gunter 1942, Caldwell and Caldwell 1972, Leatherwood 1975, Gruber 1981, Goodwin 1985). I never observed Gulf of California dolphins feeding behind these working shrimp trawlers.

Habitat use patterns—Bottlenose dolphins in the Gulf of California were sighted most often in areas close to estuaries, and the animals used these areas to feed. The use of estuarine areas as feeding sites may represent a trend in habitat use by many coastal populations of bottlenose dolphins.

Estuarine areas repeatedly have been found to be sites of high dolphin occurrence. Along the U.S. coast of the Gulf of Mexico preferred areas include ship channels, passes between inshore bays and the open ocean, river mouths, bays, lagoons, and estuarine complexes (Gunter 1942; Barham *et al.* 1980;

Table 2. Survey effort and bottlenose dolphin sightings.

Location ^a	Survey effort (days)	Dolphin schools sighted	Number of identified individuals
Bahia Agua Dulce	3	2	12
Bahia Kino	74	70	155
Punta Baja	3	1	1
Estero Tastiota	5	3	16
Guaymas	6	4	7
Isla Partida	5	3	5
Punta Willard	4	2	4
Isla Turner	11	8	6
Total	111	93	206

^a See Figure 1.

Gruber 1981; Schmidly 1981; Leatherwood and Reeves 1982, 1983*b*; Mead and Potter 1990). Along the southern California coast dolphin distribution is concentrated in areas immediately offshore of lagoon mouths and kelp beds (Hansen 1990). Off the coast of Ecuador, fishermen report frequent sightings in mangrove areas (Van Waerebeek *et al.* 1990).

In addition, behavioral observations indicate that bottlenose dolphins feed in estuarine areas. Many studies report details of feeding behavior from observations made in estuarine systems (Hoese 1971; Shane 1977, 1987; Leatherwood 1975, 1979; Gruber 1981; Irvine *et al.* 1981; Goodwin 1985). Shane (1990*a*) found that bottlenose dolphins off the west coast of Florida spent more time feeding in bay areas with seagrasses and mangroves than in surrounding Gulf waters.

Estuaries characteristically contain high concentrations of nutrients, zooplankton and fish (Moyle and Cech 1982). Presumably, it is these large concentrations of potential prey which attract dolphins to these habitats. There are two types of estuaries. The most common is a semi-enclosed coastal body of water having a free connection with the open ocean and brackish water within, resulting from a dilution of sea water with freshwater deriving from land drainage (Cameron and Pritchard 1963). Most of the embayments on the east, west and Gulf of Mexico coasts of the United States fall within this definition. A second type of estuary, often termed a negative estuary and more typical of those in the Gulf of California, receives little freshwater runoff over the course of a year, and consequently, the water in these embayments becomes progressively more saline further inland (Nybakken 1982). Despite these physical differences, both types of estuaries are sites of large concentrations of nutrients which, in turn, support great numbers of filter-feeding zooplankton and fish (Vannucci 1969, Thomson 1973).

Coastal bottlenose dolphins may specialize on estuarine species (Barros and Odell 1990). In support of this is the fact that a large proportion of the species reported as prey items are found in estuaries (Ballance 1987, Shane 1990*b*). However, bottlenose dolphins are generalists. They are found in a wide range of habitats; they prey on a large number of fishes and invertebrates; they have demonstrated the use of multiple techniques for prey capture (Gunter 1942, Caldwell and Caldwell 1972, Leatherwood 1975, Leatherwood and Reeves 1982, Shane *et al.* 1986, Barros and Odell 1990, Cockcroft and Ross 1990, Mead and Potter 1990, Shane 1990*b*). Rather than specializing on estuarine species, it is quite possible that dolphins feed in estuarine systems simply because of the high abundance of potential prey that such systems support.

Obviously, diet preferences and seasonal variations should be studied in much greater detail before estuaries can be identified as primary feeding areas for bottlenose dolphins. But estuaries are, doubtless, sites of high concentrations of fishes and invertebrates. Behavioral evidence strongly indicates that areas near estuary mouths are preferred feeding sites for Gulf of California bottlenose dolphins. And data on numbers, distribution patterns, behavior and diet indicate that this is a general trend in habitat use for many coastal populations of this species.

Ranges—The bottlenose dolphins identified in Bahia Kino were not residents

of this bay and therefore, ranged outside of this area (Ballance 1990). Thirty-nine percent of all dolphins identified in Bahia Kino were sighted there only one time. Of those individuals sighted more than once, the average time span between adjacent sightings was 30 d. And there was a notable seasonal flux of dolphins into and out of Bahia Kino.

The size of the range of several photographically identified individuals spanned a minimum of tens of kilometers of coastline. Dolphins A and B were sighted in locations separated by 25 km, dolphin #43 in locations separated by 60 km, and dolphins #29 and #112 in locations separated by 65 km.

A very small proportion of the individuals sighted in Bahia Kino also were sighted at other locations: three animals from a total of 155 identified individuals. These animals were not constant residents of Kino (Ballance 1990) and so, must have been using additional areas. Yet, they were not seen in those areas surveyed along 200 km of coastline. It is likely that with more survey effort in adjacent areas, more of the dolphins identified in Kino would have been resighted. However, one-quarter of the individuals identified in this study were sighted in these adjacent areas, and these were not dolphins that had been seen in Bahia Kino. Therefore, it seems likely that many of the animals sighted in Kino may have been ranging outside of the study area.

Several other studies indicate that ranges of coastal bottlenose dolphins can be large. Defran *et al.* (1985) reported sightings of San Diego bottlenose dolphins off the coast of Baja California. Gruber (1981) identified an animal off the coast of Texas that had previously been sighted 95 km to the southwest. Hansen (1983) resighted 12 dolphins first identified off the coast of San Diego, in locations ranging from 140 to 185 km to the north. Würsig and Würsig (1979) sighted individuals from their study population at Golfo San Jose, Argentina, 300 km away from the study area. Wolf *et al.* (1987) reported sightings of one dolphin in waters off Santa Barbara, California, and 483 km to the south off the coast of Ensenada. And Wells *et al.* (1990) reported a 1,340 km round trip for San Diego dolphins sighted in Monterey Bay.

The most detailed work on ranges of bottlenose dolphins has been conducted near Sarasota, Florida (Irvine and Wells 1972; Wells 1978, 1986; Wells *et al.* 1980; Irvine *et al.* 1981; Scott *et al.* 1990). Here, a population of approximately 100 individuals are residents of a home range area of approximately 85 km². Animals are year-round residents; immigration and emigration are rare. Animals are found in groups segregated according to age and sex, and these different segments of the population use different parts of the home range preferentially with the result that female-calf pairs, subadults and adults, males and females have varying home range sizes and locations.

Results from the present study pertain only to ranges of Gulf of California bottlenose dolphins, not to home ranges as in the Sarasota study. Still, some basic comparisons between residence patterns and ranging behavior reveal an interesting difference in site fidelity. While the dolphins in the Sarasota Bay area were residents of this region and rarely visited adjacent waters, dolphins in the mid-Gulf of California appeared to range more freely. Many dolphins visited Bahia Kino but were not continuously present in this bay (Ballance 1990).

This difference in site fidelity may be related to habitat differences (Ballance 1990). The west coast of Florida is lined with barrier islands which form numerous, large shallow bays and channels. The Gulf of California is an open coastline with few protected bays and inlets. Perhaps the large estuarine systems of the west coast of Florida support permanent prey resources and allow for resident populations of dolphins, while the smaller estuaries of the Gulf of California provide only temporary, more ephemeral prey resources, prompting dolphins to range between these areas in search of food. Additional study of residence patterns of bottlenose dolphins in differing habitat types would provide evidence to further address this possibility.

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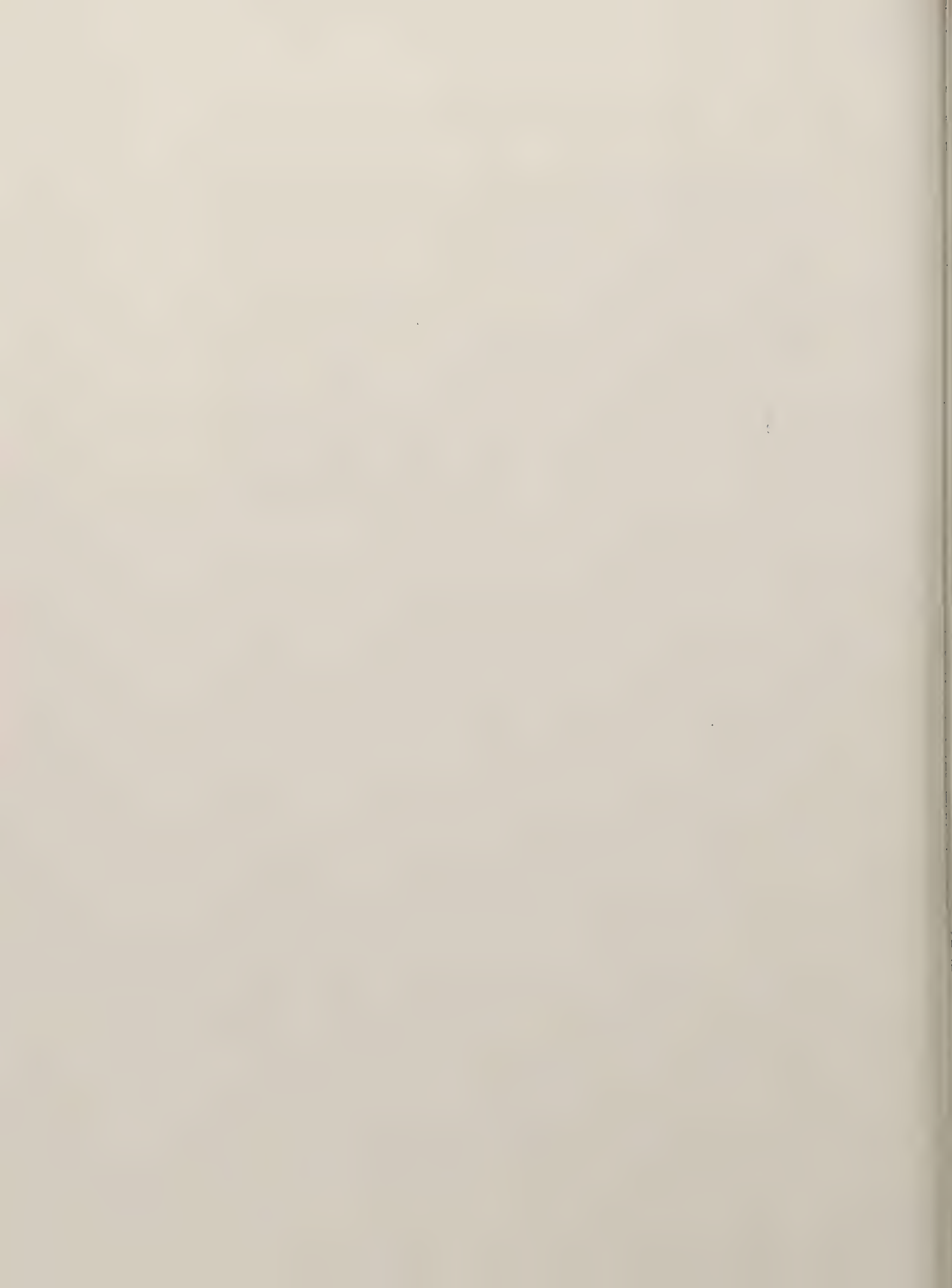
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PATHOLOGICAL FINDINGS IN THE HAWAIIAN MONK SEAL

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ABSTRACT: Postmortem examinations were performed on 45 Hawaiian monk seals (*Monachus schauinslandi*) collected during field research on the beaches of the Northwestern Hawaiian Islands (USA) from 1981 to 1985. Both males and females of all age groups, perinatal through adult, were examined. Frequent findings included parasites, trauma, cardiovascular disease (congenital and acquired), and respiratory infections. Emaciation was a common condition. All animals except neonates were infected with parasites; infection was severe in several cases. Splenic hematopoiesis was a universal histopathologic finding. Some cases exhibited lesions consistent with renal, gastrointestinal, and toxic disorders; ectopic tissue calcification; gallstones; and ophthalmologic and dental problems.

Key words: *Monachus schauinslandi*, monk seal, pathology, emaciation, parasites, trauma, survey.

INTRODUCTION

The Hawaiian monk seal (*Monachus schauinslandi*) is an endangered pinniped which lives and breeds primarily in the Northwestern Hawaiian Islands (NWHI) (USA). In the recovery plan for the monk seal, collection of baseline data on diseases was given high priority, as such data could be important to the recovery effort (Gilmartin, 1983).

While not studied extensively, parasitism of the monk seal has been documented from necropsies and examinations of fecal samples: four species of cestodes, *Diphyllobothrium hians* (Markowski, 1952) = *Bothriocephalus* sp. (Chapin, 1925), *D. elegans* and *D. cameroni* (Rausch, 1969), and *D. rauschi* (Andersen, 1987) = *D. hians* (Rausch, 1969); two nematodes, *Contracaecum turgidum* (Chapin, 1925) and *Anisakis* sp. ova recently identified in scats by Dailey et al. (1988); one acanthocephalan, *Corynosoma rauschi* (Golvan, 1959); and one lung mite, *Halarachne laysanae* (Furman and Dailey, 1980). Trematoda ova, not identified to species, also have been reported (Dailey et al., 1988). Clusters of *Contracaecum* sp. were reported attached to the ulcerated gastric mucosa of a young monk seal (Whittow and Balazs, 1979). These lesions with embedded parasites were common findings in an investigation

of mortality in monk seals at Laysan Island in 1978 (Gilmartin et al., 1980).

Serological evidence of a low incidence of calicivirus infection exists, and *Salmonella sieburg* and *S. minnesota* were isolated from rectal cultures of monk seals (Gilmartin et al., 1980; Gilmartin, unpubl. data). A toxic disease, ciguatera, also has been implicated in monk seal deaths (Gilmartin et al., 1980).

This report summarizes the necropsy findings from Hawaiian monk seals through a 5-yr period. The primary goal of compiling and examining these post-mortem data was to determine whether significant pathological processes existed which might be mitigated by management actions to enhance the recovery of this endangered species.

MATERIALS AND METHODS

Necropsies on Hawaiian monk seals were conducted and tissue specimens collected from 1981 through 1985 at most NWHI locations: Kure Atoll (28°25'N, 178°10'W), Pearl and Hermes Reef (27°55'N, 175°45'W), French Frigate Shoals (FFS) (23°45'N, 166°10'W), and Lisianski (26°02'N, 174°00'W), Laysan (25°42'N, 171°44'W), and Necker (23°35'N, 164°42'W) Islands. Research staff presence at the islands varied greatly in duration, season, and number of personnel.

Dead animals were usually necropsied where they were found by the field biologists, with

TABLE 1. Summary of pathological findings in 42 Hawaiian monk seals necropsied during 1981 to 1985.

Pathological findings	n*	Number of seals affected									
		Adult		Subadult		Juvenile		Pup		Neonate	
		Fe-male	Male	Fe-male	Male	Fe-male	Male	Fe-male	Male	Fe-male	Male
Emaciation	24	5	4	2	3	3	1	0	2	1	2
Parasitism	37	10	7	2	3	7	5	1	2	0	0
Trauma	16	4	1	1	2	0	2	0	2	1	2
Infectious disease	10	2	2	0	1	1	1	0	0	1	2
Cardiovascular disease											
Congenital	5	0	0	0	1	0	2	1	1	0	0
Acquired	5	2	2	0	0	0	1	0	0	0	0
Respiratory disease	6	0	2	0	0	1	0	0	0	1	2
Incidental findings											
Ectopic calcification	6	1	4	0	0	0	1	0	0	0	0
Ophthalmologic disorders	2	1	1	0	0	0	0	0	0	0	0
Callstones	2	2	0	0	0	0	0	0	0	0	0

* (n = the total of seals observed for each category).

abnormalities noted to the best ability of the prosector. Representative organ samples from apparently normal as well as diseased tissues were fixed in 10% buffered formalin for later histopathologic examination (Winchell, 1990). Routinely sampled tissues included lung, heart, liver, spleen, pancreas, intestine, kidney, adrenal, gonad, lymph node, muscle, and, when located, thyroid and thymus. Samples from other tissues were collected when abnormalities were suspected. Tissue samples were embedded, sectioned, and stained with hematoxylin and eosin by routine methods. Parasites collected from the digestive tract were preserved in alcohol or formalin.

Case information recorded during most necropsies included animal identification, sex, size classification (e.g., adult, subadult, juvenile, pup), necropsy date, and island. When available, historical information on individual seals was used in judging the relative importance of the histopathologic information in the overall picture of the mortality.

RESULTS AND DISCUSSION

General

Postmortem findings on 42 Hawaiian monk seals are summarized in Table 1. Findings have not been separated into primary and contributory factors, as such determinations would too often be speculative or arbitrary. Most of the listed conditions have the potential to be pri-

mary, secondary, or contributory factors in the disease process. No significant lesions were identified in three additional animals.

The necropsy data from this study suggest some categorical groupings, but these findings cannot be extrapolated to population losses because of variation in the duration of data collection among the islands, variable quality of postmortem examinations, and the very small sample (less than 5% of the estimated number of animals that died each year were recovered for necropsy). Some abbreviated case histories representing the categories in Table 1 are presented below.

Emaciation

Emaciation (lack of body fullness—characterized internally by a thin or absent fat layer, relatively thin blubber, and muscle wasting) in the seals examined was a common finding. Twenty-four of the animals were thin to severely emaciated. Early weaning and neonatal-maternal separations were the usual causes of pup emaciation. Starvation has commonly been reported in pinniped deaths (Keyes, 1965; Ridgway et al., 1975; Anderson et al., 1979; Fay et al., 1979; Dierauf, 1983). In mor-

talities with evident emaciation, it is usually difficult to determine whether malnutrition lowered resistance to disease or disease compromised an animal's ability to forage. For example, a 2- to 3-wk period of immobility and anorexia with progressive weight loss and debilitation were the primary clinical features at Laysan Island in 1978, where ciguatera and parasite infection were the probable causes of death in at least 50 seals (Gilmartin et al., 1980).

Parasitism

The intensity of parasite infection and associated lesions ranged from mild to severe; only newborn pups did not harbor gastrointestinal parasites. No new parasites were identified during the study.

The largest recorded gastric ulcer in this study was 7 cm in diameter. Usually, an animal had one or two large and many small to medium (1–3 cm) ulcers. Typically, the granulomatous scars and ulcers were more numerous in the older adults (e.g., 26 in a 17-yr-old female). No perforated ulcers were found. One juvenile seal in apparently good physical condition had parasites nearly occluding the lumen of the small bowel and had nine gastric ulcers with embedded nematodes. The ulcers were characterized by a thick pyogenic membrane overlying edematous granulation tissue. Peripheral and subserosal areas were chronically reactive with increased dense connective tissue, including large numbers of fibroblasts and histiocytes, and increased vascularity. Also evidenced was a bacteremia, probably originating from bite injuries inflicted by adult male seals. Hepatic lesions included centrilobular necrosis and fatty changes. It is difficult to ascribe a primary cause of death and determine the role of parasitism in cases such as this. Debilitation from heavy parasitism may have weakened the animal and predisposed it to attack by adult male seals and subsequent septic death, or conversely, the septic condition may have diminished parasite resistance resulting in an increased ante mortem infection.

Trauma

During the 5-yr study, the most common cause of lethal traumatic injuries (11 of 16 cases) was "mobbing" (Table 1). During a mobbing, large numbers (≤ 27) of adult male monk seals attack a single seal in mating attempts, many actually mounting the subject (Johnson and Johnson, 1981; Alcorn, 1984; Johanos and Austin, 1988). Mobbing injuries are inflicted on adult females primarily but also immature seals of both sexes. The size class and sex of 11 mobbed seals included 4 adult females, 1 subadult female, 2 juvenile females, 2 subadult males, and 2 male pups.

Mobbing incidents usually resulted in large, deep, dorsal bite wounds where skin, blubber, and sometimes muscle, were removed. The secondary effects of the bite injuries and attempted breeding included exposure, dehydration, infection, debilitation, trauma to the reproductive tract, starvation due to inability to forage, and high risk of shark predation. The eventual consequence (recovery or death) of mobbing injuries to an individual appeared unrelated to the subjectively judged gross severity of the injuries.

In addition to dorsal wounds, edema, and subcutaneous hemorrhage, three young adult (5- to 6-yr-old) females suffered traumatic damage to the reproductive tract, one of which had a severe metritis. The other two had recently ovulated and one of these had recently weaned a pup. Among the 11 mobbing victims was a 2-yr-old female with histological evidence of pubertal follicular development at the time of death.

Four of the 11 mobbing victims had chest and pulmonary lesions consistent with severe trauma. Two victims were male pups (3.5- and 4.5-mo-old), one was a yearling female, and one a 4-yr-old male. An adult male was observed mounting the 3.5-mo-old pup in shallow water, biting its back and flippers, and then leaving it in respiratory distress. Congested, hemorrhagic pulmonary tissue and severely

bruised abdominal blubber were found at necropsy of the latter seal.

Only a few incidents were documented in which trauma unrelated to male aggression was associated with mortality. Deaths of three neonates were probably related to perinatal trauma as reported in other pinnipeds (Andersen et al., 1979). Findings in the neonates included traumatic liver damage and aspirated amniotic fluid in one pup and a large quantity of blood in the thoracic and abdominal cavities of the other two pups, including a hemopericardium in one of the latter pups. A weaned male pup died after it swallowed a spiny finned fish, tail first: The fins caught in the cervical esophagus, partially obstructing it and eventually necrosing through the esophageal wall. Local infection, inflammatory reaction, and pressure-induced necrosis of the tracheal wall were observed. Small pieces of the rotted fish were identified in the bronchial tree and had caused aspiration pneumonia.

Other sources of trauma which may lead to infections and deaths are shark attack and entanglement in marine debris (Alcorn and Kam, 1986; Henderson, 1990). These appear to occur at a low frequency in the population.

Infectious disease

Infectious disease was established from findings or was suspected in 10 cases. Septicemia was histologically identified in five cases, four of which were linked to bite-wounds inflicted by adult males and included dermal abscesses and infected gastric ulcers. One of the latter group was a pup, probably infected perinatally, that died shortly after birth. The mother of this pup was sighted with an extensive back wound of mobbing origin 2 wk prior to parturition.

The only seal with a bacteremia not associated with trauma had a ruptured renal abscess. Microscopic examination of a necrotic kidney revealed severe nephrolithiasis with secondary renal abscess formation and nephrocalcinosis. A myocardial

infarction and moderate pulmonary emphysema with interstitial calcification and a heavy monocytic infiltrate were also found.

A presumed prenatal infection caused developmental abnormalities, including a grossly misshapen skull. This pup appeared uncoordinated and weak at birth (Alcorn and Buelna, 1989). Respiratory distress was punctuated by "wet" respiratory sounds and froth at the nostrils. It died at the termination of one of several convulsive episodes of increasing duration. Approximately 25% of the animal's ventrum and the entire tail were covered with granulomatous dermal nodules between 2.5 and 20.0 cm in diameter. The same type of lesion was found 3.5 cm distal to the pup's umbilicus on the umbilical cord. These nodules contained epidermal elements, including hair. The pup's eyes were affected bilaterally with buphthalmos. Glaucoma was secondary to obliteration of the Canal of Schlemm by inflammatory cells and reactive tissue. All body tissues and placenta were heavily and diffusely infiltrated with leukocytes, primarily neutrophils. Examination of pulmonary tissues revealed marked atelectasis, diffuse leukocytic infiltration, and aspirated amniotic fluid. Notably, the mother of this pup gave birth to apparently normal pups before and after this pup.

Congenital cardiovascular disease

Of five seals with congenital anomalies, two had a patent ductus arteriosus. One, a 1.5-yr-old male, died in captivity from a stress myopathy syndrome. He was found to have a 0.5 mm patency. Another juvenile male was found to have a 1.5 mm patency. A high prevalence of ductus arteriosus patencies (1.0–2.0 cm) in pups at FFS was confirmed in 1986 (W. G. Gilmartin, unpubl. data). Not all of these seals were premature. Patent ductus arteriosus was reported in several harbor seals (*Phoca vitulina*) found stranded along the Oregon coast (Stroud, 1979). It is not known

whether this is a pathologic condition in seals.

Other congenital findings included an anomalous moderator band in a subadult male, a 2.5 cm ventricular septal defect in a 4.5-wk-old female pup, and a patent foramen ovale in a 3-day-old male. The moderator band was discovered midchamber in the right ventricle, extending horizontally from the medial to lateral wall. The ventricular wall was thin (2 mm) relative to other hearts examined.

Findings in the pup with the patent foramen ovale included 200 ml of serosanguinous abdominal fluid; 50 ml of a pink-yellow pericardial fluid; congestion of the splenic, pulmonary, renal, and hepatic tissues; and splenic and hepatic hemosiderosis. The findings suggest that the patency was a significant contributing factor to the death.

Acquired cardiovascular disease

Acquired cardiovascular lesions were observed in four aged monk seals, two each, male and female, and a juvenile male. The two females were aged by their canine teeth, but all four seals exhibited physical characteristics and incidental necropsy findings consistent with old age. A 17-yr-old female had cerebral infarcts and recent laminar necrosis of the cerebral cortex with associated focal collections of neutrophils and erythrocytes. She also had severe focal arteriosclerosis with luminal occlusion in pancreatic arterioles and less severe lesions in the arterioles of the spleen and perirenal fat. Severe congestion in pulmonary and hepatic tissues was suggestive of terminal heart failure.

An old male exhibited several cardiac and vascular changes, including myocarditis, myocardial calcification, myocardial necrosis, and calcification of the internal elastic lamina of the renal artery.

The other aged male died the morning after his capture. Severe passive congestion of pulmonary tissue and a chronic focal lipid pneumonia was reported. Focal calcification of the internal elastic lamina of

the cardiac arteries and severe passive congestion with early cardiac cirrhosis of the liver were also observed. Centrilobular hepatic scarring suggested prior episodes of severe passive congestion. Hyperplasia of the vesicular and reticular adrenal cortical zones with atrophy of the glomerular zone was suggestive of a pre-neoplastic state. Adrenal changes may have led to an aberrant stress response contributing to terminal heart failure. These data suggest that age-related cardiovascular changes may be significant factors in the death of aged seals.

Mild arteriosclerosis in the spleen of a juvenile (1.5-yr-old) male was a surprising finding. The cause of death was not apparent in this animal.

Respiratory disease

Respiratory disorders included two cases of chronic pneumonia with associated pleuritis, one case of aspiration pneumonia, two prenatal pneumonias associated with generalized infectious disease, and one newborn male where considerable atelectasis and aspirated amniotic fluid were the only lesions observed.

Partial atelectasis was commonly observed in newborns. This was not related to primary lung pathology, but likely to prolonged birth, non-viable individuals who lived only a short time, or animals suffocated by the placenta or their mothers. A male, a female born with generalized infection, and a female with evidence of perinatal trauma were found to have fluid-filled lungs, possibly amniotic fluid indicative of difficult parturition.

Primary pulmonary disease of unknown etiology was believed to be the cause of death in at least two animals: a 20-yr-old male with chronic pneumonic lesions and associated pleuritis and a 5-yr-old male with severe septal congestion, interstitial edema, pleural edema, and atelectasis.

Incidental findings

Hematopoiesis was evident in all spleen samples. Neither the sex, age, nor specific

disease processes correlated with the degree of splenic hematopoiesis. In many cases, hepatic tissue was too autolyzed for the identification of hematopoietic activity, but in two cases, some hepatic hematopoiesis was evident.

Ectopic tissue calcification was found in five cases: (1) focal calcification of the intramural arteries in the uterus of an adult female; (2) calcification in the elastic lamina of coronary arterioles in an aged male; (3) focally calcified connective tissue in a fibrotic area of the adrenal gland, focal renal deposits in the medulla and basement membranes of proximal convoluted tubules, pulmonary deposits in the walls of septal blood vessels and within hyaline membranes of peripheral small bronchi—all found in the tissues of an old male; (4) focal calcification in the adrenal cortex of a 1-yr-old male with pseudogland formation in the glomerular layer and mild arteriolar sclerosis of the spleen; and (5) multiple sites of focal calcification in a 17-yr-old male seal, myocardial calcification adjacent to bacterial myocarditis with infarct and necrosis, interstitial calcification in pulmonary alveolar septa with bacterial pneumonia and emphysema, nephrocalcinosis in the kidney with abscess formation secondary to nephrolithiasis, and calcification of the internal elastic membrane of the renal artery.

Tissue calcification may be related to changes typical of old age or to disease states including chronic infection and endocrine and mineral imbalances. Primary hyperparathyroidism occurs at a low frequency in domestic and wild mammals, and lesions in these cases do not support such an etiology.

Signs of ophthalmologic disease are not commonly observed in wild monk seal populations and were also infrequently found at necropsy. Ophthalmologic problems of undetermined etiology were observed in two seals. Trauma or infectious disease were possible causes of corneal clouding in a 5-yr-old male that died of sepsis secondary to a mobbing wound. A

17-yr-old female had a central cicatricial scar on the opaque yellow cornea of one eye. Other findings included atherosclerosis, cerebral infarct, pancreatitis, and a pale yellow gallstone (1×3 mm).

In two seals, ages 17 and 24, very worn dentition was reported. This condition was probably more common than noted, although most older seals probably exhibited it. One aged male had severe osteolysis of both the mandible and maxilla, such as might be associated with root abscesses.

CONCLUSIONS

These findings are of importance to the monk seal recovery effort in that the information has led to (1) identification of some causes of mortality in the monk seal population; (2) information about general disease processes and age-related changes in monk seal organ systems; (3) compilation of a histologic data base for future evaluation of monk seal tissues; and (4) re-evaluation of postmortem procedures resulting in implementation of changes which will allow gathering of more pertinent morphologic, physiologic, and pathologic data.

The data indicate that deaths from septicemia resulting from wounds received in adult male mobbing attacks account for more monk seal deaths than were previously believed associated with this behavior. Parasitism is a usual finding, but of undeterminable significance in monk seal disease processes. Importantly, there does not appear to be any disease phenomenon affecting the population in a manner which may significantly hinder recovery of the species.

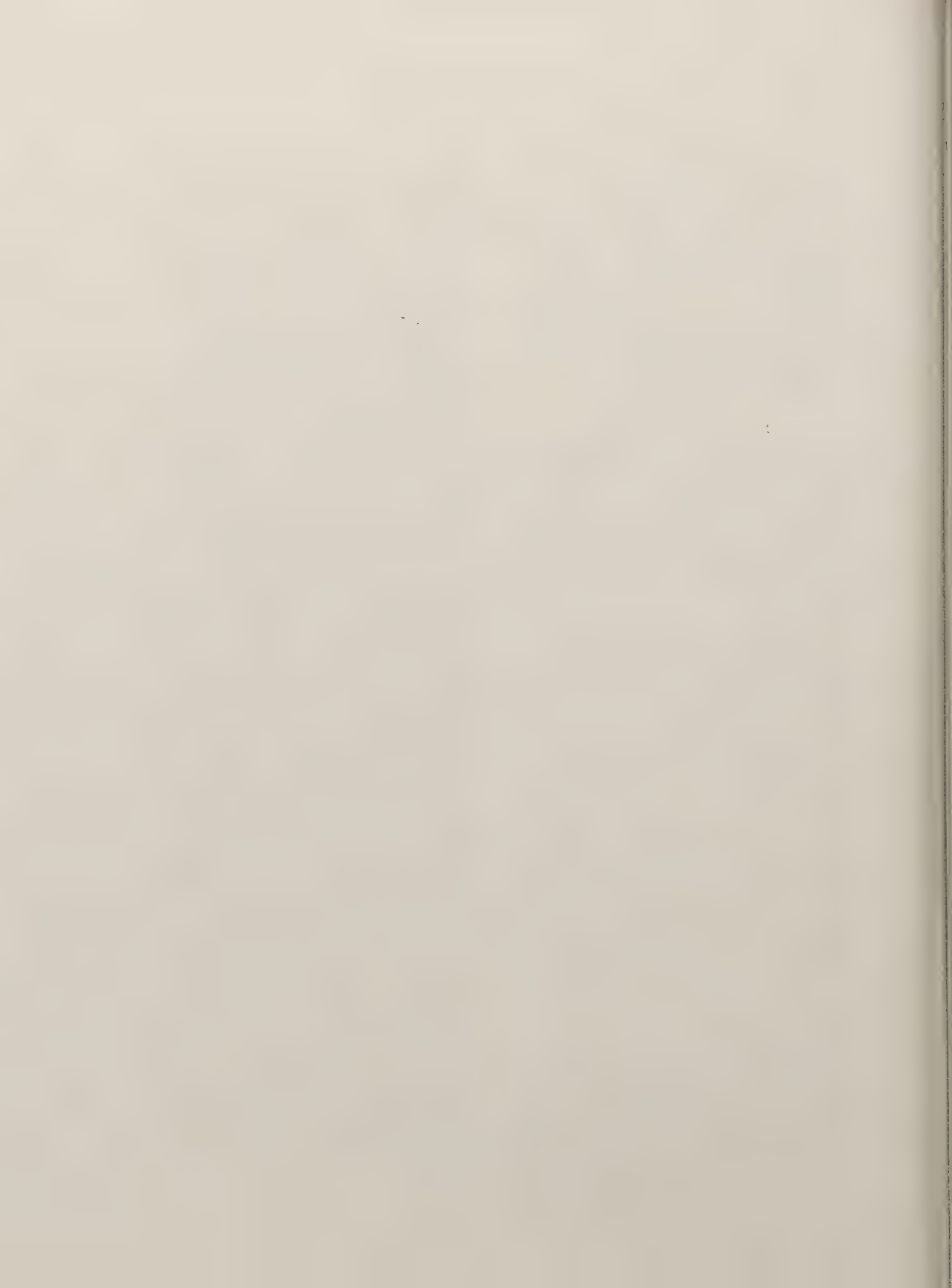
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NONLINEAR AND LOGISTIC GROWTH IN EXPERIMENTAL POPULATIONS OF GUPPIES¹

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Abstract. Previous experiments have shown that for a specific experimental system of guppies (*Poecilia reticulata*), per capita growth rate is linearly related to population biomass. A length-specific population model is developed to examine how the various mechanisms of density dependence (i.e., changes in somatic growth rates, reproductive rates, and cannibalism) act in concert to shape the overall population response to intra-specific competition. Despite many nonlinear components, equilibrium per capita growth in the model is linearly related to population biomass, mimicking the logistic growth seen in the experiment. Using the model, the components of density dependence are varied to determine how each component shapes the overall density-dependent response. Density dependence in somatic growth rates is found to be the most important population-regulating mechanism in this system. In the past, emphasis has been placed on density dependence in birth and death functions. The importance of somatic growth in shaping per capita population growth curves may be underestimated.

Key words: density dependence; guppy; intraspecific competition; logistic; nonlinear dynamics; per capita growth rate; *Poecilia*; population dynamics.

INTRODUCTION

Logistic growth refers to a particular form of density dependence in which per capita growth rate declines linearly with population size. In the early 1900s, Raymond Pearl attempted to convince a skeptical world that the logistic represented a universal law of population growth (Kingsland 1985). Subsequent studies have shown that density dependence often differs significantly from the simple, linear predictions of the logistic. Differences from the logistic are believed to be important in promoting stability between competing species of *Drosophila* in experimental systems (Gilpin and Ayala 1973, Pomerantz et al. 1980). Furthermore, evidence is accumulating that species with particular life histories, such as long-lived mammals (Fowler 1981, 1988) or species that feed higher on a food chain (May et al. 1979), deviate from the logistic growth model in a consistent, predictable manner. This is strengthened by analyses that suggest that the form of density dependence can, itself, be subject to natural selection (Gilpin et al. 1976, Gill 1978). Nonlogistic growth curves are currently being used in the management of marine mammals (Smith 1983) and other species.

For nonlogistic density dependence (e.g., the θ -logistic model of Gilpin et al. 1976), per capita growth rate is typically modeled as a nonlinear function of population size (measured in numbers of individuals or population mass). Such models suffice as empirical representations of density dependence but give little

insight into the factors that shape population growth. Increasing population size can affect somatic growth rates, survival rates, birth rates, age at maturation, etc. I will refer to these effects as the mechanisms of density dependence. The functional relationship between per capita growth rate and population density is likely to depend on which of these mechanisms function to limit population growth. For instance, Goodman (1980) showed that when the density-compensating mechanism was a linear relationship between fecundity and population size, the resulting per capita growth rate is a concave ($\theta > 1$ in the θ -logistic model), nonlinear function of population size. Kerfoot et al. (1985) showed the converse, that certain nonlinear mechanisms can result in a linear relationship between per capita growth rate and population size.

In this paper I investigate how population growth curves are shaped by various mechanisms of density dependence. I limit my investigations to actual mechanisms that were measured in an experimental system that shows logistic growth (Barlow 1982). In this system, guppy (*Poecilia reticulata*) populations experience growth limitation due to resource competition and cannibalism. Somatic growth, reproduction, and juvenile mortality were measured at a variety of different tank densities. Populations were forced to grow at constant per capita growth rates by maintaining constant per capita harvest rates (following the Smith-Gause culture dilution approach, Smith 1963). Models are fit to describe changes in these traits as continuous functions of population size. These submodels of density dependence for particular mechanisms are incorporated into an overall model that describes the dynamics of the

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populations. By changing the various submodels of density-dependent mechanisms, I determine how each of these mechanisms act in shaping overall population growth as a function of population size.

METHODS

Experimental design

Fifteen experimental populations were established in 39-L glass aquaria. Each was fed a combination of dried flake food (0.21 g dry mass Tetra Min Staple Food) and frozen *Daphnia* (0.05 g dry mass) 6 times per week. Populations were harvested at 2-wk intervals. Harvests were taken as a constant percentage of the population size and were applied randomly over all size classes. Five harvest rates were used (5, 10, 15, 20, and 25% biweekly) with three replicates at each rate. Populations were allowed to grow for a total of 36 harvest periods (72 wk) under constant conditions. Populations approached stable size-frequency distributions while growing at a constant rate (determined by the harvest rate). During the course of the experiment, information was collected on length-frequency distributions within each population, somatic growth rates, individual fecundity rates, and population sex ratios.

Brackish water was circulated continuously between the five tanks within each of the three replicates. Water was also passed through external filter boxes using gravel as a filter medium. Thermostatically controlled heaters within the filter boxes maintained tank temperature between 23° and 25°C. Half of the water in each tank was discarded every 2 wk, and the remainder was passed through a combination of a diatom and activated carbon filter and an ultraviolet sterilizer. The discarded water was replaced with a brackish mixture of 50% seawater and 50% deionized water. Overhead fluorescent lights provided a 14:10 L:D diel cycle. The entire experimental system was housed in a plywood enclosure, isolating it from changes in ambient light and temperature.

Several structures were placed within the tanks to reduce juvenile mortality due to cannibalism. Previous experiments with guppies have shown that uncontrolled cannibalism leads to cyclic populations (Breder and Coates 1932, Shoemaker 1944, Laakso 1959). Following the design of Silliman and Gutsell (1958), 10 cm wide fences were constructed from 3 mm vertical glass rods spaced 1.5 mm apart. This fence was placed diagonally across one corner of each tank to provide an absolute refuge for small fish. Very few young survived during preliminary experiments with this system, therefore additional structure was added. Eight plastic mesh baskets (1-pint [55 mL] grocery berry baskets) were placed in each tank. Juvenile survival then increased to acceptable levels. The only other structures within the tanks were the water pump intakes and siphons, which equilibrated water level between

tanks; both were screened to prevent movement of fish into the filter or between tanks.

The harvesting procedure consisted of removing a percentage of the fish present in each tank at biweekly intervals. Prior to harvests, fish were immobilized with MS-222 (ethyl-m-aminobenzoate) to facilitate handling. Population size was determined, and harvested fish were chosen randomly with respect to sex and size. Randomization and selection procedures are described by Barlow (1982). During alternate harvests (i.e., at 4-wk intervals), 35mm photographs were taken of the anesthetized fish in each population for later measurement of the length of each individual. Harvested fish were preserved in ethanol and were later used to determine length distributions, fecundity rates, and length/mass relationships. For the latter, 206 harvested fish were measured, dried, and weighed. Mass was determined to the nearest 1 mg after drying in an oven at 60°C for a minimum of 6 h.

Model design

A sex- and length-specific population projection model is formulated to describe the dynamics of the experimental system. Given initial length-frequency vectors for males and females, the model calculates the expected length-frequency vectors after one time period. The projection accounts for somatic growth (changes in length), births, adult mortality (harvest), and juvenile mortality (harvest and cannibalism). The model is purely deterministic and allows fractional representation in a length class.

Somatic growth is modeled with the Von Bertalanffy growth function. Length, L , is expressed as a function of initial length (L_i), time (t), and two parameters:

$$L(L_i, t) = L_{\infty} - [(L_{\infty} - L_i) \cdot \text{Exp}(-k \cdot t)]. \quad (1)$$

The parameter L_{∞} represents the asymptotic length, and k determines the rate at which length approaches that asymptote. The above equation is fit separately for males and females.

In the model, individuals are assigned to 1 mm length classes. To determine the growth of individuals within a length class, the expected lengths after one time interval are projected using both the minimum and maximum lengths of that length class as L_i in Eq. 1. Individuals are assigned to new length classes based on the assumption that they are uniformly distributed between the projected minima and maxima. As an example, if the 22–23 mm length class contains only one fish and if the expected lengths after one time period are 22.5 and 24.0 mm (for 22.0 and 23.0 mm fish, respectively), the single fish would be distributed as 1/3 in the 22–23 mm length class and 2/3 in the 23–24 mm length class.

As in the above example, not all the fish within a length class will necessarily enter another length class. In this case, a fraction of individuals remain in that length class indefinitely (although this fraction declines

exponentially with time). This is analogous to having nonzero elements on the principal diagonal of a population projection matrix. The effect can be minimized by having a large number of small length classes. There are, however, some desirable characteristics of having large length classes. If a group of fish of a given size is allowed to grow using the above algorithm, their size distribution would widen, thus mimicking the sort of natural variability in growth that would be expected in real populations. Length classes of 1 mm were found to be appropriate to mimic the level of individual variability seen in guppy growth (Barlow 1982).

The birth rate for mature females is modeled as a product of brood size and the rate of brood production. The birth rate, b , of a mature female of length L is thus given by:

$$b(L) = r \cdot F(L), \quad (2)$$

where r is the rate of brood production, and $F(L)$ is the brood size as a function of length. Brood size is modeled as a power function of length:

$$F(L) = \gamma \cdot L^\epsilon, \quad (3)$$

where γ and ϵ are parameters that shape the relationship between brood size and length. Females are assumed to mature at a specific length (i.e., knife-edge maturation). In the projection model, all individuals within a length class are assigned the birth rate corresponding to the midpoint of that interval. Births are distributed equally as males and females. Births are assumed to occur uniformly during the 2-wk time step of the model. Earlier births are discounted by juvenile mortality rate. Surviving young are assigned to length classes based on the assumption that they are uniformly distributed in size between the size at birth (6.5 mm) and the projected size at 2 wk (from Eq. 1).

Harvests contribute to juvenile mortality and are assumed to be the only source of adult mortality. In the model, this source of mortality is applied by multiplying the number of individuals in each length class by the escapement rate (i.e., the complement of the harvest rate).

Juvenile mortality was largely due to cannibalism. Based on observations made during the course of the experiment, the risk of mortality due to cannibalism decreases rapidly with size (Barlow 1982). Juvenile mortality is therefore modelled as an exponentially decreasing function of length. Insufficient information was gathered to estimate the rate at which cannibalism decreased with length. I assume that the risk of mortality due to cannibalism decreases by 50% with each millimetre of growth. The instantaneous rate of mortality due to cannibalism, $\mu(L)$, is thus given by:

$$\mu(L) = \mu_0 \cdot 0.5^{(L-L_0)}, \quad (4)$$

where μ_0 is the initial risk of mortality at birth, and L_0 is the size at birth. The survival rate, $s(L)$, is the complement of the death rate, $d(L)$, and represents the

fraction of juveniles in a given size class that would survive one time step:

$$s(L) = 1 - d(L) = e^{-\mu(L)}, \quad (5)$$

where length, L , is taken as the midpoint of the length class.

Total tank biomass, M , is used as the measure of population density. Tank biomass is estimated by applying a length/mass relationship to the length-frequency vector. Individual mass, m , is assumed to be a power function of length:

$$m(L) = \alpha \cdot L^\beta. \quad (6)$$

Separate length/mass relationships are used for juveniles (< 12 mm), males (> 12 mm), and females (> 12 mm).

Model parameterization

Data collected from the above experiments are used to parameterize a population projection model. Five of the parameters in the above model (L_∞ , k , γ , μ_0 , and α) are estimated as functions of population size (taken as total tank biomass). Each of these density-dependent parameters is represented as a nominal value (at zero tank biomass) minus a power function of tank biomass:

$$f(M) = f_0 - p_1 \cdot M^{p_2}. \quad (7)$$

Parameters of this density-dependent function are fit stepwise for each of the five model parameters. First, the nominal value, f_0 , is fit with $p_1 = 0$. Two parameters, f_0 and p_1 , are then fit with $p_2 = 1$. Finally all three are fit simultaneously. This stepwise addition of terms proceeds until the reduction in explained variance is no longer significant (F test). Parameters are fit via nonlinear least squares based on the Simplex algorithm (Press et al. 1988).

Total tank biomass is estimated from the measured length-frequency distributions and a fitted relationship between mass and length. This approach is complicated because the length/mass relationships for mature males and females were, themselves, significantly dependent on population biomass (Barlow 1982). Therefore, an iterative approach is used. First, overall length/mass relationships are estimated for males and females (irrespective of tank biomass) based on measured lengths and dry masses. From this, preliminary estimates of tank biomass are made. The density-dependent length/mass relationships are then estimated by making α (Eq. 6) a function of tank biomass (per Eq. 7). Tank biomass is re-estimated. The process of first estimating parameter values and then estimating biomass is repeated until parameter estimates converge.

Somatic growth rates are estimated separately for males and females based on successive measures of distinctly marked fish. Distinctive marks included color patterns in males and caudal pigmentation and "golden" phenotype in some females (Barlow 1982). Data include 1098 measures of paired lengths, typically

TABLE 1. Parameters estimated for the various submodels within the population growth model. The value f_0 represents the nominal value at zero population biomass. Values p_1 and p_2 represent density-dependent modifications to the nominal values as per Eq. 7. Asterisks indicate values that did not add significantly to the goodness of fit. Missing values indicate values for which no attempt was made to fit.

Model	Parameter	f_0	p_1	p_2
Female growth (Eq. 1)	L_∞	37	2.04	2.23
	k	0.12	0.04	*
Male growth (Eq. 1)	L_∞	17	1.03	*
	k	0.24	0.08	*
Brood size (Eq. 3)	γ	1.31×10^{-4}	0.19×10^{-4}	1.97
	ϵ	3.67		
Juvenile survival (Eq. 4)	μ_0	0.73	0.007	6.51
Female mass (Eq. 6)	α	5.09×10^{-6}	1.28×10^{-6}	*
	β	3.19		
Male mass (Eq. 6)	α	3.11×10^{-6}	0.23×10^{-6}	*
	β	3.25		
Juvenile mass (Eq. 6)	α	2.83×10^{-6}	*	*
	β	3.20		

measured from photographs taken 4 wk apart. Parameters L_∞ and k (Eq. 1) are estimated to minimize the sum of squared residuals between observed and expected lengths. Both parameters are allowed to vary as functions of tank biomass, alternating the stepwise addition of terms (p_1 and p_2) between L_∞ and k . The nominal value (f_0) for L_∞ is fixed at 38 mm for females and 17 mm for males; these were the largest individuals measured during the course of the experiment.

The rate of brood production (r in Eq. 2) is estimated as the fraction of mature females that contained distinct embryos (eyespot stage or later) divided by the ontogenetic time required between formation of the eyespot and birth. The fraction of females with embryos was previously estimated by dissecting harvested individuals; this fraction, 0.574, did not vary with population biomass (Barlow 1982). In another series of experiments, the development time between eyespot and birth was measured as 16 d, and it also did not vary with tank biomass (Barlow 1982). The rate of brood production is thus 0.036/d or 0.502/harvest period (27.9 d between broods).

Brood sizes are estimated as a function of female length based on the number of mature eggs and developing embryos seen in dissections of harvested females. Females matured at an average length of 15 mm, and maturation length showed no consistent changes with population biomass (Barlow 1982). The brood size function (Eq. 3) is fit based on brood sizes of 661 mature females (15–38 mm).

Juvenile mortality due to cannibalism could not be measured directly. The juvenile mortality parameter, μ_0 , is estimated by minimizing the discrepancies between the observed population growth trajectories and those predicted from the population growth model. The length–frequency distributions were measured in the experimental populations at 4-wk intervals. The predicted length–frequency distribution at the end of each interval is calculated by applying two iterations

of the model to the length–frequency at the beginning of the interval. The parameter, μ_0 , is chosen to minimize the squared deviations between the predicted and observed length–frequency distributions. This mortality parameter is allowed to vary as a function of population biomass (per Eq. 7).

Population growth curves

Per capita population growth curves are calculated from the above model by choosing a value for the harvest rate, h , and projecting an arbitrary length–frequency distribution until it reaches a stable population size and length distribution. This process is repeated over a wide range of harvest rates. Per capita growth rate, g , is calculated from harvest rate, h , as

$$g = \frac{1}{(1-h)} - 1.0. \quad (8)$$

A sustainable harvest rate of 0.25 (25% per harvest period) would thus correspond to a per capita growth rate of 0.33 (33% per harvest period).

RESULTS

Length/mass relationships

Length/mass relationships were strongly density-dependent for females, less so for males, and not significantly so for juveniles (Fig. 1). The greater effect in females was largely due to density-dependent fecundity and the mass that developing eggs add to total female mass. The stepwise fitting method indicated that the power parameter (p_2 , Eq. 7) is not needed to adequately fit the term α of the length/mass relationship as a function of population biomass for either females or males (Table 1). No density-dependent parameters are needed to adequately fit the length/mass relationship for juveniles. For females, males, and juveniles, mass increases at approximately the 3.2 power of length (β in Table 1).

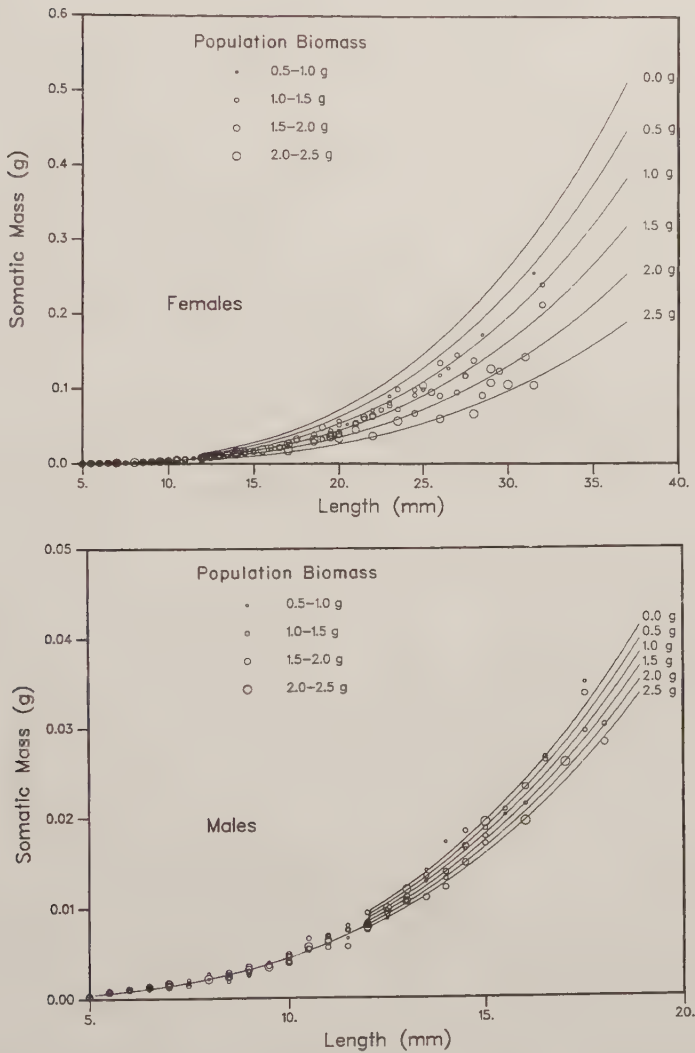


FIG. 1. Somatic mass for females and males expressed as a function of length and population biomass. Illustrated are the observed values for four different ranges of population biomass (O's) and fitted values (—) for six different population sizes (total tank guppy biomasses in grams).

Population biomass

Population biomass is estimated from observed length-frequency distributions and the fitted length/mass relationships. Trajectories of mean population biomass are shown in Fig. 2. Population biomass appears relatively stable at the higher harvest rates, but at lower harvest rates, the trajectories of population biomass are concave downward. Mean population biomasses for the last 10 harvest periods were 1.81, 1.65, 1.38, 1.29, and 0.96 g (for harvest rates of 5, 10, 15, 20, and 25%, respectively).

Somatic growth rates

Somatic growth rates are strongly density dependent for females and for males (Fig. 3). The stepwise fitting method indicates that the power parameter (p_2 , Eq. 7) is not needed to fit the growth parameter, k , but is needed to model changes in asymptotic length as a function of population biomass. The time required to reach sexual maturity in males (≈ 12 mm) varies from 8 wk at a population biomass of 0.5 g to 26 wk at a population biomass of 2.0 g. The time required to reach sexual maturity in females (15 mm) varies from 7 wk

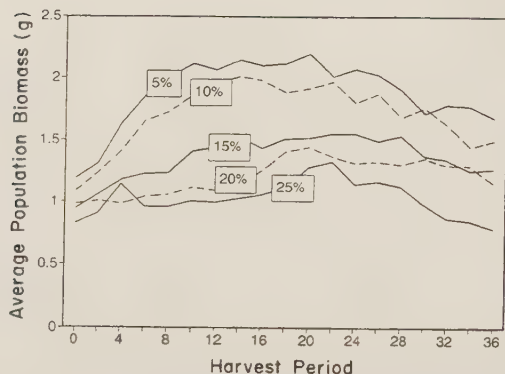


FIG. 2. Mean population biomass during the course of the experiment for harvest rates of 5, 10, 15, 20, and 25%. Values represent means of three populations with the given harvest rate.

at a population biomass of 0.5 g to 38 wk at a population biomass of 2.0 g.

Brood size

Brood size is also strongly affected by population biomass (Fig. 4). Both density-dependent parameters p_1 and p_2 are required to adequately fit the brood size parameter, γ , as a function of population biomass (Table 1). Brood size increases at approximately the 3.7 power of length, thus increasing in proportion to body mass (which increases at only the 3.2 power of length).

Juvenile survival rates

The nonharvest component of juvenile survival (mostly cannibalism) shows a high degree of density dependence. The exponent of the density response function, p_2 , is 6.5 (Table 1), indicating a highly nonlinear response. This is illustrated in Fig. 5, which shows survival rates to be the same at biomasses of 0.0, 0.5, and 1.0 g but decreasing rapidly from biomasses of 1.5–2.5 g.

Population growth rates

Incorporating all aspects of density dependence in the model, the resulting population growth curve is illustrated by the solid line in Fig. 6 (as a function of population biomass). This population growth curve is almost indistinguishable from a logistic growth curve. Per capita growth can be represented as a linear function of population biomass. The only deviation from linearity occurs near zero population biomass. (Little confidence can be put in this extrapolation to zero because parameters were fit based only on population biomasses ranging from 0.5 to 2.5 g.)

Patterns are similar when mean population biomasses for the last 10 harvest periods are plotted as a function of per capita growth rate (Fig. 6). These data

also suggest a linear relationship between biomass and per capita growth. A regression line for the empirical data differs in slope and position from the curve predicted by the model. This could be explained by errors in estimating the 25 parameters that comprise the growth model. It is also likely that the mean biomass for the last 10 harvest periods does not represent the equilibrium biomass for the given harvest rates. Population biomasses appear to have overshoot equilibrium for harvest rates of 5, 10, and 15%. Populations may have been in stages of oscillatory approach to equilibrium at the time the experiment ended. Qualitatively, the experiment and model show strikingly similar results.

Alternative population growth curves are calculated based on several scenarios for density dependence (Fig. 7). These include: (1) using a mean fecundity curve without density dependence, (2) using a mean growth rate without density dependence, and (3) using a mean juvenile survival without density dependence.

DISCUSSION

In this simple experimental system, population growth is controlled simultaneously by several density-dependent mechanisms, including reproductive rate, somatic growth rate, and cannibalism. Furthermore, these mechanisms are essentially nonlinear. The best mathematical representations I have found for these mechanisms are nonlinear equations whose parameters are functions (in some cases nonlinear functions) of population biomass. Therefore, it might be viewed as somewhat surprising to find that per capita growth rate is essentially a linear function of population biomass. The combined effect of all the density-compensatory mechanisms is not distinguishable from the simple predictions of the logistic growth curve.

Similar results have been noted before. Three independent studies show that for *Daphnia*, brood size is a concave, nonlinear function of population size (Frank et al. 1957, Smith and Cooper 1982, Kerfoot et al. 1985). In two of these studies, however, per capita population growth is linearly related to population size (Kerfoot et al. 1985). In the third study, per capita growth rate was, like brood size, a concave, nonlinear function of population size (Smith et al. 1988). The lesson is clear. As emphasized by Kerfoot et al. (1985), one must not assume that nonlinearity in a single density-dependent factor will result in nonlinearity in the overall per capita growth curve.

As with the *Daphnia* studies cited above, different studies with guppies have shown different shapes of per capita growth curves. In experiments that were similar to that of Barlow (1982), Silliman and Gutsell (1958) and Silliman (1968) found that per capita growth rates for guppy populations were concave, nonlinear functions of population biomass. Differences in experimental protocol may be responsible for this difference in results. In particular, the harvest scheme of

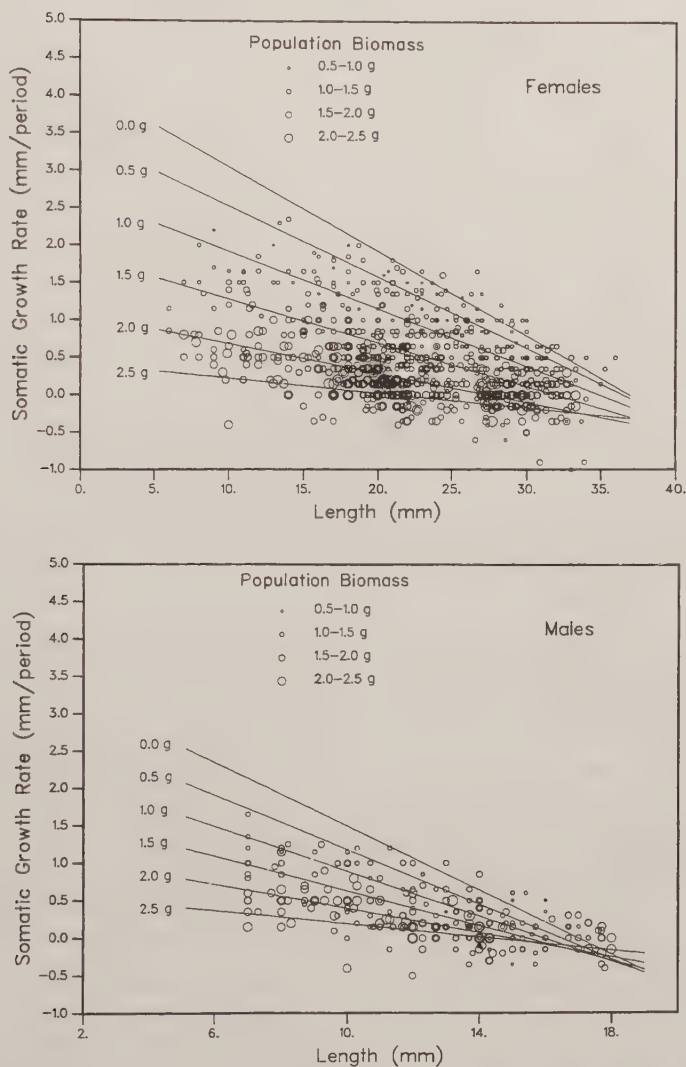


FIG. 3. Somatic growth rate of females and males (expressed in millimetres per 2-wk harvest period) as a function of length and population biomass. Illustrated are the observed values for four different ranges of population biomass (O's) and fitted values (—) for six different population sizes (biomasses in grams).

Silliman and Gutsell (1958) and Silliman (1968) did not include harvest of juveniles. Using a population model, Barlow (1982) showed that this discrepancy in results can be explained solely on the basis of this difference in experimental methods. It is likely that by comparing contradictory experimental results we can learn about how various factors affect density dependence. Instead of quibbling about which experimental protocol is "better" (Smith et al. 1988), we should be asking ourselves whether any generalities can be gleaned by reconciling apparently contradictory results.

In addition to the above lesson, that the sum of many nonlinear effects can be essentially linear, my experiment and model illustrate another important point. All proximate mechanisms of density dependence do not contribute equally to shaping the overall density-dependent response of a population.

As mentioned above, somatic growth, reproductive rates, and cannibalism rates all showed significant changes with population size. By systematically eliminating each of these as density-regulating mechanisms in the model, I examined the role played by each in

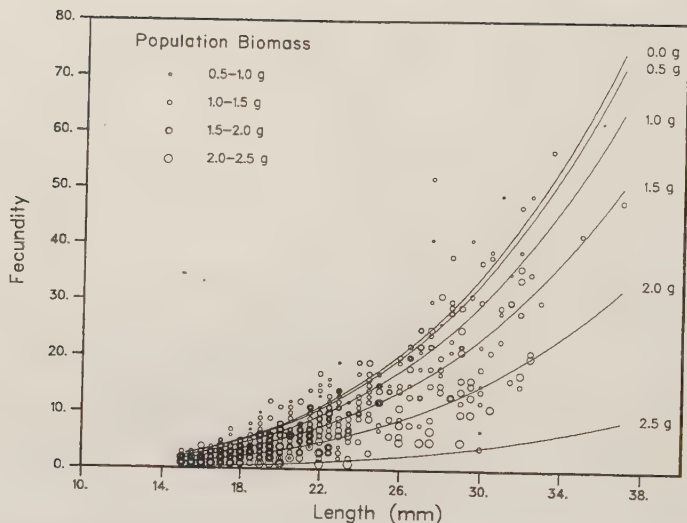


FIG. 4. Brood size (fecundity) expressed as a function of female length and population biomass. Illustrated are the observed values for four different ranges of population biomass (O's) and fitted values (—) for six different population sizes (biomasses in grams).

shaping the overall density-dependent response of the population. Using the full model, per capita growth rate was linearly related to population size. Modifications of the model can be compared to this linear or logistic growth curve.

Density-dependent components of the model were eliminated, one by one, by substituting the mean parameters for the density-dependent parameters given in Table 1. Models without density dependence in reproductive rates and cannibalism rates did not show appreciable change in the overall shape of the per capita

growth curve (Fig. 7). Both could be adequately represented by a logistic growth curve (although there is a slight tendency for the model without density-dependent reproduction to be concave downward). When density dependence in somatic growth rates was eliminated from the model, the population growth curve changed considerably (Fig. 7). In the resulting model, per capita growth rate was essentially constant up to approximately half of carrying capacity, and then decreased rapidly.

The framework for discussing components of density

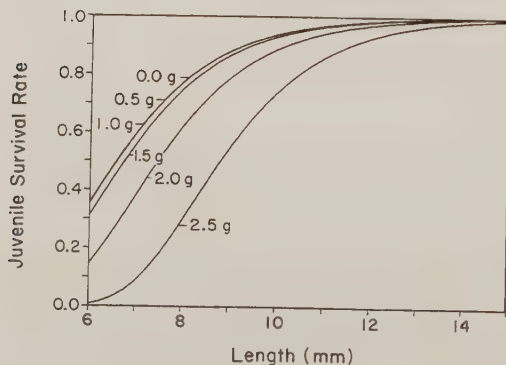


FIG. 5. Juvenile survival rate (excluding the harvest component of mortality) expressed as a function of length and population biomass. Illustrated are fitted values for six different population sizes (biomasses in grams). Survival rates were not measured directly, rather parameter values were chosen to give the best fit of the population growth model to the observed population trajectories.

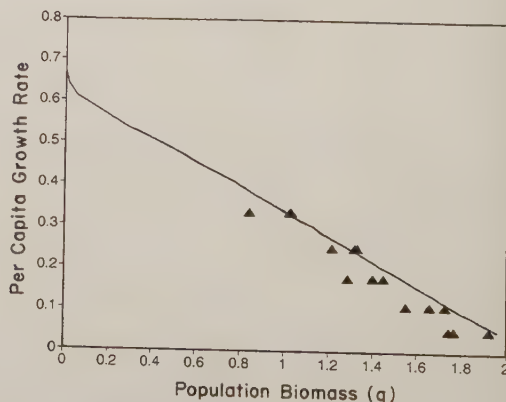


FIG. 6. Equilibrium population biomass and population size as functions of per capita growth rate (as defined by harvest rate) for the experiment, Δ , and for the model (—). Equilibrium population biomasses for the experiment are estimated as the mean values for the last 10 harvest periods.

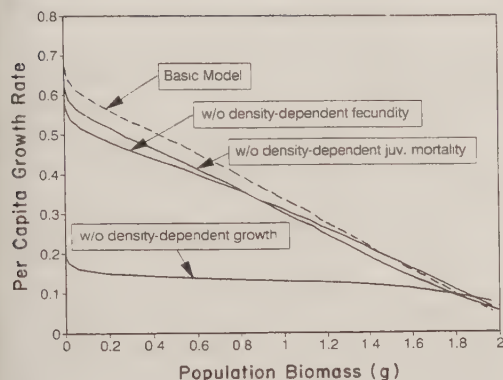


FIG. 7. Equilibrium population biomass as a function of per capita growth rate (as defined by harvest rate) for the basic model and for three special cases of the model: (1) excluding (w/o = without) density dependence in brood size, (2) excluding density dependence in growth rates, and (3) excluding density dependence in juvenile survival rates.

dependence has typically centered on birth rates and death rates (b and d , Kerfoot et al. 1985). Somatic growth rates affect overall b and d , even though length-specific rates, $b(L)$ and $d(L)$, are not affected by growth rates. By growing slower, juveniles remain at a vulnerable size for a longer period, thus increasing their risk of mortality by cannibalism. Similarly, slow growth reduces effective fecundity by making females smaller at any given age. As was seen in Fig. 7, density dependence could be eliminated in length-specific fecundity or in juvenile survival rates without appreciably changing the shape of the density-dependent response. At least with species that show indeterminate growth, such as fish, somatic growth rates are likely to be very important in shaping per capita growth curves.

The importance of density dependence in somatic growth rates has been noted previously by several researchers working on fish and amphibian populations. Wilbur (1977) showed that increasing tadpole density did not affect larval toad survival rates but greatly affected the probability of surviving from egg to metamorphosis via its effect on somatic growth rates. In a near natural pond, Werner et al. (1983) showed that the somatic growth rate of bluegill fish (*Lepomis macrochirus*) is affected by predatory fish density. The latter work not only indicates the importance of plasticity in fish growth rates outside the laboratory, but also emphasizes the trade-off between optimal foraging (and high growth rate) and the potential for predatory mortality. Similar trade-offs may have existed between growth rate and cannibalism for juvenile guppies in my experimental system.

As a final note, I want to emphasize an often ignored point regarding density dependence in population growth. Numerical abundance and biomass have both been used as measures of population size in population

growth models. Fisheries data are typically in units of biomass (such as tons of fish landed); hence, most fisheries population models are expressed in terms of biomass (Schaefer 1954, Ricker 1958, Pella and Tomlinson 1969, etc.). To terrestrial ecologists, population size is typically taken to mean numerical abundance (Gilpin and Ayala 1973, May 1974, Goh 1977, etc.). In fact, the same models are used by both groups whether referring to numbers or biomass (Pomerantz et al. 1980). To further complicate matters, those who have made predictions regarding the expected shape of population growth curves have failed to specify whether their predictions apply only to numbers, to biomass, or to both (Gilpin and Ayala 1973, Gilpin et al. 1976, May et al. 1979, Fowler 1981).

In fact, however, the units of measure do matter. Although a full explanation would require another paper, it is worth noting that the per capita growth curve from the experiment described here looks very different when expressed as a function of population number rather than biomass (Barlow 1982). The reason is that the size-frequency distributions are not the same at different population growth rates. Because mass is nonlinearly related to length, total population number will not be linearly related to population biomass unless the size-frequency distribution does not change. If the size-frequency distribution does change with different population growth rates, per capita growth rate cannot be linearly related to both population number and biomass.

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RECENT POPULATION TRENDS AND ABUNDANCE ESTIMATES FOR THE PACIFIC SARDINE (*SARDINOPS SAGAX*)

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ABSTRACT

Five different analytical approaches and several sources of data were used to investigate current sardine abundance and recent changes in population size. Each analysis and all available information show an increasing trend in sardine abundance since the late 1970s. Current estimates indicate that the 1990 spawning biomass fell within the range of 60,000 to 210,000 metric tons (MT). Greater precision may be required for population estimates as a commercial fishery develops. We suggest that an integrated method of stock assessment that combines fishery-dependent and fishery-independent data will best meet future stock assessment and management needs.

RESUMEN

Se investigó la abundancia y cambios recientes en el tamaño de la población de la sardina utilizando cinco enfoques analíticos y varias fuentes de datos. Tanto la información disponible como cada uno de los análisis revelaron que desde finales de los 70 la abundancia mostró una tendencia al alza. Estimaciones recientes indican que en 1990 la biomasa de los reproductores que desovaron fué de entre 60,000 a 210,000 toneladas métricas; las estimaciones podrían requerir mayor precisión al desarrollarse la pesquería comercial. Sugerimos que para satisfacer necesidades futuras de evaluación de stock y manejo se considere un método de evaluación de stock integrado, que combine datos dependientes e independientes de la pesquería.

INTRODUCTION

One characteristic of sardine resources (genera *Sardinops* and *Sardina*) is that the populations can fluctuate widely. Scale-deposition rates for Pacific sardines (*Sardinops sagax*) in California Bight anoxic sediment indicate such fluctuations (Soutar and Isaacs 1974). Depth-related variations in the numbers of sardine scales in sediment suggest periodic changes of significant magnitude in relative abun-

dance, extending back over the past 200 years (Smith and Moser 1988). The study of Pacific sardine population dynamics has also indicated large changes in abundance during this century (Murphy 1966; MacCall 1979). Adjacent year classes have been shown to vary in numbers by more than an order of magnitude (Murphy 1966), presenting the potential for rapid increases or decreases in overall population size, should trends in recruitment develop.

The Pacific sardine resource off the west coast of North America currently extends from the northern part of California to central Baja California. A large fishery was supported by the Pacific sardine many decades ago, when the population ranged from Canada to Mexico. However, abundance declined dramatically from 1945 through 1965 (with some short-lived reversals), and the fishery collapsed (Radovich 1982). In 1967 a moratorium was placed on the taking of sardines along the California coast because of the depressed condition of the stock. Annual landings were negligible from then until recent years, when sardines were once again regularly encountered by California and northern Baja California fishermen.

In 1985 the sardine spawning biomass was estimated to have increased to at least 18,140 MT (Wolf and Smith 1986), and a catch quota of 907 MT was established, allowing a small directed fishery in the United States. At the same time, bait fisheries were allocated a separate quota of 544 MT per year. Total directed and bait fishery quotas were increased to 8,165 MT for the 1991 season in recognition of the continued expansion of the resource. In addition to the directed and bait fisheries, current management regulations allow a 35% maximum incidental take of sardines (by weight) in the California fishery for Pacific mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*). Sardine by-catch in the mackerel fishery usually amounts to about 1,000–3,000 MT per year.

A fishery outside the control of United States authorities operates in Ensenada, Mexico, and proba-

bly harvests the same sardine stock as the southern California fishery. Ensenada sardine landings dominated the fishery in 1990, but were roughly similar in volume to those in the United States during most other recent years (table 1).

In response to apparent increases in sardine abundance and associated public interest in expanding the commercial fishery, a workshop was convened in September 1990 by the California Department of Fish and Game (CDFG) to develop recommendations for assessing and managing the resource. An objective of the workshop was to examine various sources of data concerning the status of sardines. In this paper, we review five independent and complementary analyses used by workshop participants to evaluate the current state of the population. The data, methods, and analyses reported here incorporate some improvements introduced as a result of work done since the workshop. Data employed in the analyses are described in the next section, followed by an explanation of methods and results for each approach. We compare results in the final section and suggest an approach for future assessment of the stock.

DATA

Several sources of information were available. Some were relatively long time series extending back over decades; others were more recent in scope, or fragmentary. Direct estimates of sardine biomass from virtual population analyses (VPA) were available for 1932–59 in Murphy 1966 and for 1945–65 in MacCall 1979. Biomass estimates from MacCall 1979 were used for years when estimates from both sources were available (table 2). No direct VPA biomass estimates were available for years after 1965.

The two general categories of information about sardine biomass during recent years are described in

detail below. The first category consisted of data types similar to catch-per-unit-effort (egg density, larval density, and tons of sardine sighted per block by fish spotters); the second category consisted of indices that measured sardine biomass by means of presence-absence data (proportion of sea-survey stations positive for eggs and larvae, counts of blocks where sardines were seen by fish spotters, and counts of positive tows from CDFG sea-survey data).

Catch-per-unit-effort (CPUE) indices have lately received much criticism as tools for measuring relative abundance of pelagic fish like sardines because CPUE tends to decline more slowly than abundance (i.e., relationships between CPUE and biomass tend to be nonlinear: see Bannerot and Austin 1983 and references therein). Theory underlying the use of indices of abundance based on presence-absence data is described by Smith (1990), Mangel and Smith (1990), and Wolf and Smith (1985). As with CPUE data, it is possible that indices derived from presence-absence data do not change proportionally with abundance. This is a concern, particularly when data were collected from a geographic area smaller than the range of the stock.

California Cooperative Oceanic Fisheries Investigations

MacCall and Prager (1988) used an analysis of variance approach (ANOVA) to derive an index of abundance for Pacific sardine larvae sampled by California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys from 1951 to 1985. Their ANOVA model consisted of independent additive month, region, and year factors combined to estimate the log of the mean density of larvae in each month, region, and year. MacCall and Prager used antilogs of year factors from the ANOVA to obtain index values of relative annual larval abundance (table 2). This time series is especially valuable because it spans the decline of the 1950s and 1960s, the unfished low period of the 1970s, and the early recovery of the 1980s.

For this study, we used four additional types of CalCOFI data: estimates of sardine egg density (eggs/0.05 m²); estimates of larval sardine density (larvae/0.05 m²); the fraction of sampling stations at which eggs were found ("proportion positive for eggs"); and the fraction of stations at which larvae were found ("proportion positive for larvae"). These data were for winter and spring cruises (one cruise per year during January to March and one cruise per year during April to June) and probably covered the period of peak spawning for sardines. The data were

TABLE 1
Annual Sardine Landings (MT) for Ensenada (Mexico)
and California (U.S.), 1983–1990

Year	Ensenada	California			Grand total
		Directed	Incidental	Total	
1983	274	192	353	545	819
1984	0	61	238	299	299
1985	3722	14	593	607	4329
1986	243	421	762	1183	1426
1987	2432	600	1711	2311	4743
1988	2035	1034	2801	3835	5870
1989	6224	1400	4409	5809	12033
1990	11375	2035	1329	3364	14739

Data sources were the Instituto Nacional de Pesca for Ensenada; LMR Fisheries Research, Inc. for the 1989 incidental landings; and the California Department of Fish and Game for all other California landings.

TABLE 2
Data Used in Analyses for Sardine

Year	Number stations	E	L	PE	PL	VPA	SQUIRE	LO	CDFG	ANOVA	WTS	SPT
1916	—	—	—	—	—	—	—	—	—	—	—	16.56
1917	—	—	—	—	—	—	—	—	—	—	—	16.68
1918	—	—	—	—	—	—	—	—	—	—	—	17.35
1919	—	—	—	—	—	—	—	—	—	—	—	16.85
1920	—	—	—	—	—	—	—	—	—	—	—	16.51
1921	—	—	—	—	—	—	—	—	—	—	—	16.50
1922	—	—	—	—	—	—	—	—	—	—	—	16.43
1923	—	—	—	—	—	—	—	—	—	—	—	17.33
1924	—	—	—	—	—	—	—	—	—	—	—	16.52
1925	—	—	—	—	—	—	—	—	—	—	—	16.96
1926	—	—	—	—	—	—	—	—	—	—	—	18.03
1927	—	—	—	—	—	—	—	—	—	—	—	16.84
1928	—	—	—	—	—	—	—	—	—	—	—	16.69
1929	—	—	—	—	—	—	—	—	—	—	—	17.14
1930	—	—	—	—	—	—	—	—	—	—	—	17.40
1931	—	—	—	—	—	—	—	—	—	—	—	18.45
1932	—	—	—	—	—	3,524	—	—	—	—	—	16.27
1933	—	—	—	—	—	3,415	—	—	—	—	—	15.62
1934	—	—	—	—	—	3,625	—	—	—	—	—	17.49
1935	—	—	—	—	—	2,845	—	—	—	—	—	16.67
1936	—	—	—	—	—	1,688	—	—	—	—	—	17.57
1937	—	—	—	—	—	1,207	—	—	—	—	—	17.00
1938	—	—	—	—	—	1,201	—	—	—	—	—	16.64
1939	—	—	—	—	—	1,608	—	—	—	—	—	17.13
1940	240	699.10	49.13	0.75	0.81	1,760	—	—	—	—	—	17.32
1941	210	336.90	36.88	0.63	0.75	2,457	—	—	—	—	—	17.62
1942	—	—	—	—	—	2,065	—	—	—	—	—	16.96
1943	—	—	—	—	—	1,677	—	—	—	—	—	16.95
1944	—	—	—	—	—	1,260	—	—	—	—	—	16.45
1945	—	—	—	—	—	720	—	—	—	—	—	16.57
1946	—	—	—	—	—	566	—	—	—	—	—	16.79
1947	—	—	—	—	—	405	—	—	—	—	—	16.85
1948	—	—	—	—	—	740	—	—	—	—	—	16.03
1949	—	—	—	—	—	793	—	—	—	—	—	16.48
1950	—	—	—	—	—	780	—	—	—	—	—	16.36
1951	96	33.33	2.06	0.17	0.15	277	—	—	—	16.75	1.00	16.59
1952	152	6.85	3.49	0.10	0.11	136	—	—	—	4.66	1.00	16.23
1953	226	0.21	0.07	0.03	0.01	202	—	—	—	0.48	1.00	16.20

(continued on next page)

"Number stations" is the total number of stations (tows) for CalCOFI data. E is mean number of eggs per 0.05 sq. m. L is mean number of larvae per 0.05 sq. m. PE is proportion of CalCOFI stations positive for sardine eggs. PL is proportion of stations positive for sardine larvae. VPA is biomass (thousand MT) of sardines age two and older from a virtual population analysis. SQUIRE is a catch-per-unit-effort-like index (short tons sighted per block) from fish spotters for nighttime flights over a core area where sardines are normally abundant. LO is the number of blocks in which sardines were spotted by fish spotters during each year. CDFG is California Department of Fish and Game sea-survey data (n.mi.²). ANOVA is analysis-of-variance data from MacCall and Prager 1988; the original ANOVA data were logarithms but are given here in arithmetic units. WTS is for weights from MacCall and Prager (1988, table 2) used to scale the ANOVA data. SPT is for mean annual sea-surface temperatures (centigrade) at Scripps Pier. The symbol — indicates no data available.

from an area of the California Bight much smaller than the historical range of sardines; the boundaries were chosen to coincide with the boundaries of the ichthyoplankton survey conducted during 1941 (figure 3 in Smith 1990). Data for 1940–89 were obtained from table 1 in Smith 1990 and augmented to include data for 1990 (Paul Smith, NMFS, Southwest Fisheries Science Center, pers. comm.). There were 30 observations for each type of CalCOFI data, and a total of 120 CalCOFI observations (table 2).

CalCOFI cruises and sampling procedures are explained in Hewitt 1988. No cruises were conducted in some years, and the number of sampling stations

in the study area varied from one survey year to the next. Distance between sampling stations was too great to precisely measure the density of sardine eggs and larvae at low biomass levels. Fortunately, indices of relative abundance based on presence/absence of eggs and larvae are expected to be more robust than density estimates at low biomass and sampling levels (Smith 1990; Mangel and Smith 1990).

Fish-Spotter Data

Fish spotters are pilots employed by commercial fishermen to locate, identify, direct the harvest of,

TABLE 2 *continued*
Data Used in Analyses for Sardine

Year	Number stations	E	L	PE	PL	VPA	SQUIRE	LO	CDFG	ANOVA	WTS	SPT
1954	219	39.67	11.98	0.15	0.11	239	—	—	—	104.79	1.00	16.81
1955	142	26.87	7.29	0.17	0.09	170	—	—	—	19.77	1.00	16.50
1956	156	47.88	6.90	0.09	0.05	108	—	—	—	3.50	1.00	16.37
1957	145	23.00	12.09	0.10	0.10	90	—	—	—	6.62	1.00	17.36
1958	171	86.38	8.86	0.30	0.31	177	—	—	—	7.79	1.00	17.84
1959	188	182.00	7.88	0.29	0.25	122	—	—	—	6.85	1.00	18.35
1960	197	117.14	4.47	0.18	0.17	88	—	—	—	2.25	1.00	16.61
1961	73	17.08	1.40	0.16	0.08	54	—	—	—	0.39	0.66	16.52
1962	64	1.77	0.95	0.02	0.05	27	—	6	—	1.04	0.48	16.24
1963	77	14.22	1.94	0.05	0.04	21	1.38	51	—	0.95	0.65	16.96
1964	183	0.43	0.00	0.02	0.01	11	1.31	36	—	0.06	0.57	16.42
1965	112	4.57	0.79	0.11	0.10	3	0.02	10	—	0.93	0.66	16.52
1966	169	2.01	0.29	0.01	0.05	—	0.03	9	—	0.25	1.00	17.00
1967	—	—	—	—	—	—	0.00	0	—	0.12	0.28	16.92
1968	—	—	—	—	—	—	0.01	2	—	—	—	16.93
1969	147	0.33	0.26	0.03	0.04	—	0.00	0	—	0.90	0.86	16.64
1970	—	—	—	—	—	—	0.00	4	—	—	—	16.62
1971	—	—	—	—	—	—	0.00	6	—	—	—	16.18
1972	118	0.00	0.03	0.00	0.01	—	0.00	1	—	0.07	0.54	16.87
1973	—	—	—	—	—	—	0.00	2	—	—	—	16.45
1974	—	—	—	—	—	—	0.00	0	—	—	—	16.47
1975	267	2.54	0.07	0.03	0.01	—	0.00	0	—	0.03	0.71	15.53
1976	—	—	—	—	—	—	0.00	0	—	—	—	17.26
1977	—	—	—	—	—	—	0.00	0	—	—	—	17.25
1978	189	0.38	0.18	0.03	0.02	—	0.00	0	—	0.11	0.87	17.42
1979	—	—	—	—	—	—	0.00	0	—	—	—	16.85
1980	—	—	—	—	—	—	0.00	0	—	—	—	16.62
1981	139	0.99	0.23	0.03	0.01	—	0.00	2	—	0.52	0.89	17.62
1982	—	—	—	—	—	—	0.24	8	—	0.09	0.19	17.12
1983	—	—	—	—	—	—	0.33	15	—	2.34	0.10	17.97
1984	141	3.40	6.50	0.06	0.04	—	2.77	20	—	0.62	0.89	18.31
1985	99	10.96	8.80	0.06	0.05	—	97.36	61	670	21.07	0.30	17.21
1986	183	3.45	3.62	0.01	0.04	—	32.35	58	970	—	—	17.72
1987	81	18.73	23.00	0.06	0.11	—	20.12	85	1,850	—	—	17.56
1988	85	40.75	2.25	0.08	0.05	—	145.75	109	2,508	—	—	16.99
1989	72	61.00	4.96	0.11	0.17	—	34.84	78	3,680	—	—	17.18
1990	66	77.89	5.71	0.03	0.08	—	39.03	80	1,480	—	—	17.88
1991	—	—	—	—	—	—	—	—	3,840	—	—	16.97

and estimate the size of fish schools (Squire 1961, 1972). Analogous to CalCOFI data, two indices of relative abundance based on fish spotter data were available: densities of sardines observed by fish spotters, and the proportion of total blocks searched by fish spotters in which sardines were observed (table 2).

An index of relative density (biomass per block sighted by fish spotters in each year) was calculated from flights conducted at night over a "core" area where sardines were relatively abundant (Squire 1972). There were 28 annual records for the period 1963–90 (table 2). Unpublished sardine density data from fish spotters used in this analysis were developed and provided by Jim Squire (NMFS, Southwest Fisheries Science Center, pers. comm.).

N. C. H. Lo (NMFS, Southwest Fisheries Science Center, pers. comm.) developed the proportion-positive-blocks index of relative abundance. Lo's index was calculated by counting "positive blocks"

for sardines from 1962 to 1990 (29 annual records) where positive blocks were unique blocks in which sardines were seen by fish spotters (e.g., sardines were seen in six blocks by fish spotters during 1962; table 2). The proportion-positive index from fish-spotter data was calculated annually from all flights. Fish spotters covered a broader geographic area than the sardine stock in each year (N. C. H. Lo, unpublished data) so that counts of positive blocks were measures of the areal extent and size of the sardine stock.

Landings

Sardines commonly occur both in "pure" schools (sardines only) and in "mixed" schools with Pacific or jack mackerel. In recent years, incidental sardine catches in the mackerel fishery were a primary source of sardines in the southern California landings (table 1).

In 1988, LMR Fisheries Research, Inc. instituted a

program to collect fishery-based data other than tons landed. Each year from 1988 through 1990, data were collected from the San Pedro fresh fish market and a Terminal Island cannery. Samples were collected at both locations during the directed sardine fishery in January, and during the year-round mackerel fishery. Species composition data were collected from about 30.5% of all wetfish fleet landings during the study period. When sardines were present, biological samples consisting of 25 randomly selected fish were collected from individual deliveries. These fish were measured (standard length to the nearest mm, appendix table A), weighed (round weight to the nearest 0.1 g, appendix table B), and examined for sex and maturity. Otoliths were removed for age determination (appendix table C). Ages were estimated by examining otoliths with reflected light under $18\times$ magnification (Sunada, undated; Mosher 1954).

The fishery data included information about the volume and age composition of landings during 1988–90, but were not suitable for standard VPA-based population estimates because the time series of catch-at-age data were short, and cumulative fishing mortalities during recent years may have been low (Pope 1972).

Sardine Egg Survey

From 1985 to 1991, CDFG conducted annual sea surveys to collect sardine eggs (Wolf and Smith 1986; Wolf et al. 1987). The extent of spawning area, defined by the number of sampling stations at which sardine eggs were found, was used to measure the areal extent and relative size of the spawning biomass. This approach allowed managers to track trends in biomass levels while the sardine population was relatively small and difficult to measure with conventional techniques (Wolf and Smith 1985). Smith's (1990) results and other analyses described in this paper indicate that spawning area is a useful index of biomass for sardines. Spawning area estimates for 1985–91 are given in table 2.

CDFG sea-survey design and sampling techniques are discussed in Wolf and Smith 1985 and 1986. Surveys were designed to take place during peak spawning and to cover waters in which spawning was likely to occur. The geographic extent of the surveys varied somewhat each year to accommodate new information about the range of sardine spawning. After the 1986 survey, which used a dense station plan over a relatively small area (Wolf et al. 1987), surveys encompassed the Southern California Bight and adjacent waters. Because the survey area increased slightly each year, a minor portion of the

increase in observed spawning area may be due to eggs detected in areas not surveyed the year before. Also, spawning was observed at the edge of the survey grid in some years, indicating that some fish may have spawned outside the survey area. However, annual CalCOFI surveys (which cover a larger area) found few sardine eggs outside the areas identified by CDFG surveys during each year for 1985–91 (unpublished data), indicating that the actual spawning area was probably identified by the CDFG surveys each year.

Sea-Surface Temperatures (SST)

Scripps Pier SST data, which are the longest time series of uninterrupted oceanographic data for Pacific sardine habitat, were used in this analysis (table 2). MacCall and Prager (1988) identified three major regimes in the data for 1916 to the late 1980s: warm water from 1916 to the early 1940s, followed by cool water until the mid-1970s, and then warm water until the late 1980s. Additional data through 1991 indicate that warm conditions have continued.

METHODS AND RESULTS

Indices used in our analyses to measure sardine biomass (table 2) were generally consistent with one another and indicated similar trends in abundance. Correlation coefficients were positive except in two cases where the sample size was small (table 3). Correlations among CalCOFI indices and between VPA biomass estimates and CalCOFI indices were particularly high (correlation coefficients >0.8). Correlation coefficients between other pairs of indices were also high but not reliable because sample sizes were small.

Historical CalCOFI Larval Abundance

MacCall's (1979) VPA estimates of sardine biomass were used to calibrate MacCall and Prager's (1988) CalCOFI larval index to units of sardine biomass (age 2 and older). The two data sets overlap from 1951 to 1965, but with incomplete monthly and regional coverage by the 1961–65 CalCOFI surveys. Index values from MacCall and Prager's 1988 ANOVA model were scaled by a multiplicative constant (25,072 MT) so that the index had the same weighted geometric mean and units of measurement as VPA biomasses over the period of overlap. Weights were taken from table 2 of MacCall and Prager 1988; data for 1951–60 were given unit weight, and weights for 1961–65 ranged from 0.482 to 0.659 (table 2).

VPA spawning biomass estimates and scaled CalCOFI index values are shown in figure 1. Index

TABLE 3
Correlation Coefficients for Indices Used to Measure Sardine Biomass in a General Linear Model

	E	L	PE	PL	VPA	SQUIRE	LO
L	0.88 (30)						
PE	0.92 (30)	0.87 (30)					
PL	0.93 (30)	0.89 (30)	0.98 (30)				
VPA	0.81 (17)	0.91 (17)	0.89 (17)	0.93 (17)			
SQUIRE	0.47 (16)	0.22 (16)	0.36 (16)	0.20 (16)	0.86 (3)		
LO	0.74 (16)	0.57 (16)	0.44 (16)	0.54 (16)	0.091 (3)	0.78 (28)	
CDFG	0.56 (6)	-0.13 (6)	0.82 (6)	0.79 (6)	*	-0.006 (6)	0.56 (6)

Column and row headings are defined in table 2. Sample sizes are given in parentheses. The asterisk is used where there was insufficient data to calculate a correlation.

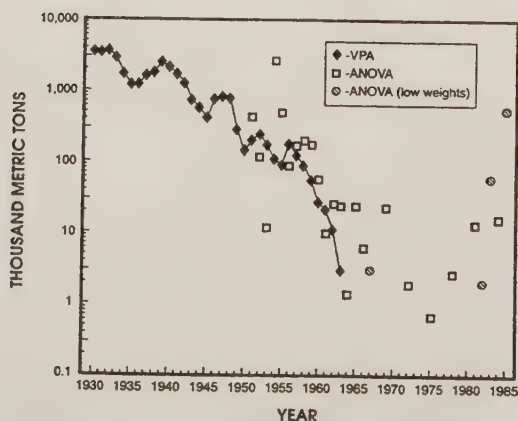


Figure 1. Sardine biomass (age 2 and older) estimated by VPA and ANOVA. ANOVA estimates are based on CalCOFI data and have been rescaled to the same units as VPA estimates. Circles indicate ANOVA estimates that are unreliable because of inadequate sampling (low-weight years).

values based on less than 30% coverage of the spawning months and regions (i.e., with weights <0.30) should be assumed unreliable. The remaining larval index values are still very imprecise, since errors appear as large as tenfold in some years. Nonetheless, long-term trends are clearly apparent in the time series of index values. The sardine population reached bottom during the mid-1970s. The recovery seems to have started in the late 1970s, but is not clearly apparent until the early 1980s.

General Linear Model Analysis

All of the data types in table 2 (with the exceptions of "Number Stations," "ANOVA," "WTS," and "SPT") were used in a statistical model to estimate recent levels of sardine biomass. The model was:

$$B_{i,y} = T_i Y_y z_{i,y} \quad (1)$$

where $B_{i,y}$ was biomass (in absolute or relative units) of sardines in year y as measured by data type i ; T_i was the effect for data type i ; Y_y was the effect for year y ; and $z_{i,y}$ was a statistical error. Taking logs gave the linear form:

$$\ln(B_{i,y}) = \ln(T_i) + \ln(Y_y) + \ln(z_{i,y}) \quad (2)$$

which was the same as would be assumed in a two-way analysis of variance on log-transformed sardine biomass data with data types and years as factors. Statistical interactions between years and data types were not considered when equation 2 was fitted because of the scarcity of data for some years and to avoid complications in interpreting the results. Interactions are, however, biologically plausible and have been demonstrated elsewhere (MacCall and Prager 1988).

Models like equation 2 are known as general linear models or log-linear models. They are often used by fishery scientists and managers to derive a single index of relative abundance for a fish population from two or more types of data (e.g., catch rates from two types of fishing vessels) or data that were similar but collected from two or more temporal or spatial strata (Gulland 1956; Robson 1966; Kimura 1981, 1988; MacCall and Prager 1988). The general linear model (2) was fitted by standard linear regression techniques (Weisberg 1980) including residual plots, outlier analyses, and Cook's (1977, 1979) distance.

Statistical errors ($z_{i,y}$) in the general linear model (2) were assumed to be independent and lognormally distributed with variance constant over years

(y) and data types (i). The assumptions of normality and constant variance were required primarily for interpretation of statistical tests, which were not an important part of the analysis. The assumption of independence was more important (see below).

Abundance estimates for each year from model 2 were expressed in the same units as VPA biomass estimates (weight of sardines age 2 and older). The expected value for log-scale biomass was computed as:

$$\beta_{VPA,y} = \tau_{VPA} + \Omega_y \quad (3)$$

where $\beta_{VPA,y}$ was the estimate of log-scale VPA biomass for sardines [$\ln(B_{VPA,y})$] from model 2 for year y ; τ_{VPA} was the estimate of the log-scale effect for VPA data [$\ln(T_{VPA})$]; and Ω_y was the estimate of the log-scale effect for year y [$\ln(Y_y)$]. Estimates of the expected value for sardine biomass on an arithmetic scale were obtained by taking exponents:

$$\Phi_{VPA,y} = \exp(\beta_{VPA,y} + \sigma^2/2) \quad (4)$$

where $\Phi_{VPA,y}$ (which estimates $B_{VPA,y}$) is the index for year y (units MT of fish age 2 and older), and σ^2 is the variance of residuals from the fit of model 2. The factor $\sigma^2/2$ corrects for bias due to log transformation (Beauchamp and Olson 1973). An unbiased estimate of median biomass can be obtained from equation 4 by neglecting the correction factor.

Variances for log-scale indices of sardine biomass were calculated from sums of variances and covariances for estimates of parameters on the right-hand side of equation 3, which were obtained from the regression output. Arithmetic-scale confidence intervals for estimates of sardine biomass in each year were calculated from the log-scale confidence intervals by taking exponents and correcting for bias as in equation 4.

The CalCOFI and fish-spotter data used to fit the general linear model (2) were probably not completely independent, since all of the CalCOFI indices were based on data collected during the same ichthyoplankton surveys, and both fish-spotter indices were derived from data collected during the same flights. The practical consequence of this problem would be biased estimates of biomass for sardines, because the statistical errors for CalCOFI or fish-spotter indices in a particular year ($z_{i,y}$) would tend to be either all positive or all negative and would not "cancel each other out." The magnitude of this problem could not be determined from the available data, but it is necessary to consider potential bias when interpreting results.

We used weights for CalCOFI data when fitting model 2 in an effort to avoid potential problems with lack of independence. Weights used were 0.5 for CalCOFI data and 1.0 for all other data types, so that each CalCOFI observation would receive half the weight used for VPA, fish-spotter, or CDFG sea-survey data during parameter estimation. We considered it unnecessary to use weights to account for lack of independence among the two types of fish-spotter indices, because differences in their geographic and temporal scope should result in some degree of independence.

Model 2 was initially fit to data for all available years, but residual plots indicated nonlinear relationships between sardine biomass and most of the indices. The initial estimate of sardine biomass during 1990 was 200,000 MT. In order to limit bias from the linear model due to nonlinear relationships in the data, we omitted years for which the initial sardine biomass estimate was much smaller (<50,000 MT during 1964–83) or much larger (>500,000 MT during 1940–41) than the 1990 level, and fitted the model again. This approach confined the analysis to a range of sardine biomass levels within which the linear model was approximately valid. An additional advantage in excluding years with very low biomass is that "zeroes" (e.g., egg density data for 1972) were not used to estimate parameters. When zeroes are present, a positive constant must be added to all observations before the data are log-transformed (e.g., MacCall and Prager 1988). Approaches to choosing additive constants are well developed when log-linear models are used for hypothesis testing (Berry 1987) but not for estimation or measurement.

Model 2 was fitted to the data for 1951–63 and 1984–90 after data for high and low biomass years were omitted, and one anomalous observation (VPA biomass in 1953) was identified as an outlier (t test = 4.43, Bonferroni probability value for mistakenly rejecting the null hypothesis of no outlier <0.05; see Weisberg 1980). The model was fitted again after the outlier was omitted. There were 114 observations in the data set finally used.

Effects of years and data types were statistically significant (probability of no differences among years or data types <0.00). There were seven observations with large standardized residuals (absolute magnitude greater than 2.0), but none could be rejected as an outlier on statistical grounds. No observations had an unusually large influence on predicted values as indicated by Cook's distance. Standard deviations for residuals from the seven data types were similar.

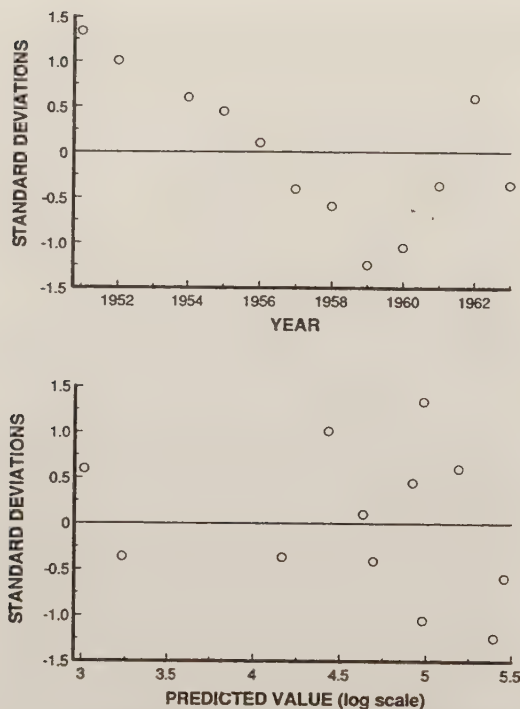


Figure 2. Studentized residuals from a general linear model. Residuals for sardine VPA data are plotted against year (top) and predicted log sardine biomass (bottom). Positive residuals occur where predicted values are too small; negative residuals occur where predicted values are too large.

Residual plots indicated that the linear model (2) was adequate for the reduced data set, although there was a trend in the plot of residual values for the VPA data versus time with predicted values being smaller than observed values (positive residuals) for 1940–55 (figure 2). This result indicates that estimates of VPA biomass for sardines from the model were generally too small (biased low) for 1951–55 and too high (biased high) for 1957–65.

Estimates of sardine biomass ($\Phi_{VPA,y}$) from the general linear model (table 4 and figure 3) indicated that sardine biomass increased after 1984, although the trend was somewhat erratic. Sardine biomass increased from about 30,000 MT in 1984 to about 160,000 MT in 1988–89 and then fell to 115,000 MT in 1990. These results were similar to trends reported by MacCall (1979), MacCall and Prager (1988), and Smith (1990), although similarity would be expected since the same data were used. Confidence intervals for the estimates of sardine biomass were quite broad, particularly for years in which sardine biomass was estimated to be large (figure 3). The

TABLE 4
Sardine Biomass Estimates from GLM Analysis
(Thousand MT of Fish Age Two and Older), with Upper
and Lower Bounds for 95% Confidence Intervals

Year	Lo 95%	Biomass	Hi 95%
1951	84	176	371
1952	48	101	213
1953	2	6	14
1954	103	216	455
1955	79	166	349
1956	59	124	261
1957	63	132	278
1958	135	284	597
1959	127	267	561
1960	83	176	370
1961	37	78	164
1962	12	24	52
1963	16	30	58
1984	14	30	65
1985	49	99	202
1986	28	57	117
1987	58	119	243
1988	78	160	326
1989	78	160	326
1990	62	115	214

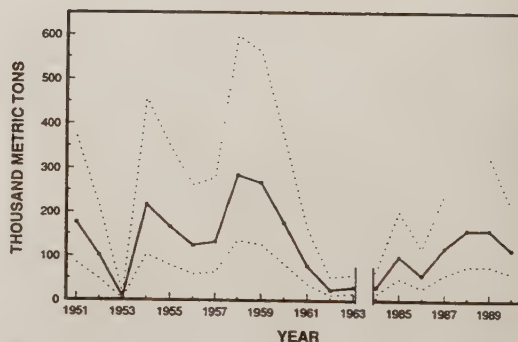


Figure 3. Sardine biomass estimates (age 2 and older) with 95% confidence intervals from a general linear model.

95% confidence interval for sardine biomass during 1990 was 62,000–214,000 MT.

Egg Production Area Method

Since 1985, CDFG has used an egg production area method (Wolf and Smith 1985) and sea-survey data (table 2) to determine if sardine spawning biomass exceeded the 18,156-MT level necessary to allow a directed fishery. The area over which a specified or "threshold" spawning biomass would be expected to occur was:

$$A = \frac{B R F S m}{P_o k W}, \quad (5)$$

where A is the spawning area occupied by the sardine population at biomass B , in nautical miles² (n.mi.²); B is the spawning biomass (MT); P_0 is the daily egg production, number eggs/0.05 m²/day; W is the average weight of mature females (g); R is the sex ratio (fraction female, by weight); F is the batch fecundity (number eggs spawned/mature female/batch); S is the fraction mature females spawning per day; k is the conversion factor from g to MT; and m is the conversion factor from 0.05 m² to n.mi.². Equation 5 is derived from the original egg production method formula (equation 4 in Parker 1985) that expresses spawning biomass as a function of spawning area and other variables (Wolf and Smith 1986).

If the observed spawning area was equal to or greater than the threshold spawning area, then a quota was allotted for directed fishing. Using estimates for the parameters in equation 5, and assuming a sex ratio of 50% females by weight (table 5), the spawning area corresponding to 18,156 MT is 2,300 n.mi.² (7,900 km²). This may be an underestimate of threshold spawning area, since females may constitute slightly more than 50% of the population by weight. The estimate of 62% for sex ratio was based on a small number of samples and is assumed to be high. The observed spawning area exceeded the 2,300-n.mi.² threshold in 1988, 1989, and 1991.

Sardine spawning area increased in each year after 1986, except in 1990 when it dropped below the level observed in 1987 (figure 4). The spawning biomass for sardines during 1990 (estimated by inverting

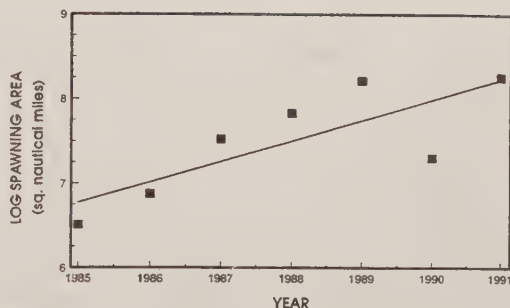


Figure 4. Sardine spawning area from CDFG sea surveys, 1985-91. Line was fitted by linear regression.

equation 5) that corresponds to the observed spawning area of 1,480 n.mi.² (5,083 km²) is 12,000 MT. This estimate seems low relative to total sardine landings during 1990 (14,739 MT) as well as to biomass estimates from other sources for 1989 and 1990. Apparently the current best estimates for the parameters in equation 5 are imprecise, or the parameter values have changed over time. Additional research will be required if this approach is used in the future.

Linear regression was used to fit a line to the CDFG sea-survey data, with years as the independent variable, and the natural logarithm of relative spawning areas as the dependent variable (figure 4). Log-transformed spawning-area data increased in an approximately linear fashion during 1986-91, indicating that sardine spawning biomass increased exponentially. If the slope of the log-scale linear regression is b , then $\exp(b) - 1$ gives the average percent annual increase in spawning area from 1986 to 1991. The estimate of b obtained from the regression (0.242) corresponds to an average annual increase of 27% in sardine spawning area and biomass. The 95% confidence interval for the average annual increase was 8%-50%.

TABLE 5

Best Estimates for Parameters Used to Estimate Area Occupied by Spawning Sardines at the Threshold Level of Spawning Biomass (18,156 MT or 20,000 Short Tons)

Parameter	Symbol	Best estimate and units
Sex ratio	R	
Measured		62% females, by weight
Assumed		50%
Batch fecundity	F	62,500 eggs/batch/ mature female/day
Spawning fraction	S	11.5% spawning females/mature females/day
Conversion factor (0.05 m ² to n.mi. ²)	m	1.458×10^{-8} n.mi. ² / 0.05 m ²
Conversion factor (0.05 m ² to km ²)	m_1	5×10^{-4} km ² /0.05 m ²
Egg production	P_0	2.4 eggs/0.05 m ² /day
Conversion factor (g to MT)	k	1×10^{-6} MT/g
Female weight	W	172 g

Life-Table Estimates

Sardine abundance during 1989 was estimated by simulation in a life table using three types of data: age composition of landings, tons landed, and CDFG estimates of spawning area. The most important assumptions in the simulation were that recruitment increased at a constant rate for the 1981-87 year classes and that total mortality rates for sardine did not change from 1983 to 1989.

Age-composition data for 1988-90 were combined because data and catch curves for individual years were similar, as would be expected under conditions such as those assumed for the simulation

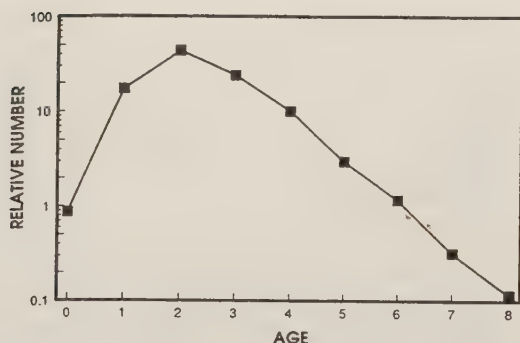


Figure 5. Sardine catch curve from commercial landings in southern California, 1988-90.

(Ricker 1975). Sardines age 3 and older were fully recruited to the fishery (figure 5 and appendix table C). The slope of the catch curve for fully recruited sardines during 1988-90 estimated by Heinke's method (Ricker 1975) from the combined data set was $Z_a = 1.13 \text{ yr}^{-1}$. If the number of sardine recruits had been constant in recent years, then 1.13 yr^{-1} would be a reasonable estimate of the actual instantaneous mortality rate (Z) experienced by fully recruited individuals in the stock. The assumption of constant recruitment was not plausible, however, because CDFG sea-survey data indicate that sardine spawning area and biomass increased by about 549% from 1986 to 1989. Density-dependent effects on recruits per unit of spawning biomass are thought to be minimal at low biomass levels, so it is likely that recruitment increased in proportion to spawning biomass and spawning area. Consequently, the slope of the catch curve (Z_a) was greater than the actual mortality experienced by the fully recruited ages (Z).

A simulated life table was constructed to account for the effect of increasing recruitment on age composition of landings and the slope of the catch curve. Recruitment in the life table was assumed to increase at a constant but unknown rate for the 1981-87 year classes, which were present as age-2 and older fish during 1983-89. The number of age-2 sardines in the simulation during 1989 (the 1987 year class) was assigned the arbitrary value of 100, and the number of recruits in previous years was calculated assuming a constant proportional rate of increase (α). Once the number of recruits in each year was specified, and assuming constant mortality (Z), the number of sardines in each year class from 1983 to 1989 could be calculated by standard methods:

$$N_{a,t} = N_{a-1,t-1} e^{-Z} \text{ and} \quad (6)$$

$$R_t = N_{2,t} = 100/\alpha^{1989-t} \quad (7)$$

where $N_{a,t}$ is the number of fish age a ($a > 2$) in year t (e.g., 1987); R_t is the number of recruits (2-year-old sardines) in year t ; Z is the total mortality rate; and α is the proportional annual increase for recruitment.

We converted relative numbers of fish in each age during each year to relative biomass for each age group using mean weight-at-age data for sardines taken by the commercial fishery from 1988 to 1990:

$$B_{a,t} = N_{a,t} w_a \quad (8)$$

where w_a is the weight of fish age a . We derived weight at age from data in appendix B by using the mean of the monthly values for each year, then using the mean of the three annual estimates to obtain w_a .

	Age						
	2	3	4	5	6	7	8
w_a (Average weight [g] per fish)	139.1	161.8	173.5	181.5	193.3	191.6	192.8

Relative total biomass in each year was obtained by summing $B_{a,t}$ for each age. Relative spawning biomass in each year was calculated from relative biomass at age, assuming that one-half of sardines age 2 spawn and that all sardines age 3 and older spawn (Clark 1934; MacGregor 1957). We calculated the slope of the catch curve (Z_a) for sardines in the simulation by applying Heinke's method to the simulated age-composition data for 1988 to 1989.

We used an iterative approach to systematically vary the annual increase in recruitment (α) in the simulation until the ratio of spawning biomass in 1985 and in 1989 agreed with that actually observed. For each iteration we specified a new value of α , and adjusted the mortality rate in the model until the slope of the actual and simulated catch curves matched exactly. The simple ratio of beginning/ending year biomasses was suitable for solving the iteration because annual spawning area increased at a nearly constant rate from 1985 to 1989, making it unnecessary to match biomass estimates for each year in between. Intermediate years were fit by the simulation because of the assumption that recruitment also increased at a constant rate during those years. The closest match between the observed and simulated data was for $\alpha = 160\%$ and $Z = 0.65 \text{ yr}^{-1}$.

	Observed	Life-table simulation
Ratio 1985/1989		
spawning biomass	549%	535%
Slope from catch curves	1.13	1.13

An estimate of the fishing mortality rate (F) for sardines during 1983–89 was obtained from the estimate of total mortality:

$$F = Z - M \quad (9)$$

where M is the rate of natural mortality. The rate of natural mortality (M) for sardines is uncertain. Murphy (1966) and MacCall (1979) used $M = 0.4 \text{ yr}^{-1}$ for VPA analyses, although Murphy used $M = 0.8 \text{ yr}^{-1}$ for 1951 and later year classes. In this analysis we used a range of $0.3\text{--}0.6 \text{ yr}^{-1}$ for M . Biomass in 1989 was calculated from the ratio of fishing mortality rate (annualized) and landings:

$$B_a = C/F \quad (10)$$

where B_a is the average biomass (MT) and C is total landings during 1989. Sardine landings during 1989 (C), assuming that the southern California and Ensenada fisheries exploit the same stock, amounted to 12,033 MT, and biomass estimates for 1989 ranged from 41,000 to 247,000 MT.

Z	M	F	Biomass (landings/ F)
0.65	0.3	0.35	40,747
0.65	0.4	0.25	54,399
0.65	0.5	0.15	86,387
0.65	0.6	0.05	246,727

No particular value of M within the indicated range is thought to be the best estimate under current conditions. However, for the specific purpose of comparison with the historical biomass estimates given in table 2, the current biomass estimate associated with $M = 0.4$ (54,399 MT) is probably the most appropriate, because it is based on the same estimate of M that was adopted for the earlier VPA analyses.

The precision of life-table estimates for sardine biomass was not calculated, because the number of observations used to fit the model (spawning area in 1985 and 1989) were too few to obtain meaningful results from approaches based on asymptotic theory or bootstrap methods.

Factors Affecting Sardine Biomass

There has been a long and colorful debate (Radovich 1982) about the relative importance of environment, ecology, and fishing on short- and long-term changes in sardine abundance (Smith and Moser 1988). Water temperatures are believed to affect abundance (Radovich 1982), although a variety of other environmental factors have also been identified (Kondo 1980). The transition from warm to cold water in the early 1940s corresponds approximately to the decline in abundance at that time.

Data and results from our analyses, and new Scripps Pier temperature data extend the historical record for sardines (figure 6). Like the historical data, our new data indicate that water temperatures and fishing both affect abundance. The historical record (pre-1965) indicates that sardine biomass decreased in the late 1930s and early 1940s, when exploitation increased beyond 20% annually and sea-surface temperatures declined to or below the historical average (16.9°C). Exploitation rates during 1941–65, when sardine biomass declined consistently, were generally higher than 30% and, in 1958, as high as 68%. Temperatures during the same period were generally well below the historical average except during the 1957–59 El Niño.

Data and results for recent years (1965 and after) indicate that sardine biomass remained low during 1965–74, when recorded landings were nil and temperatures were generally below average. Biomass began to increase in about the late 1970s, when water temperatures increased beyond the historical average and exploitation rates remained near zero. Sardine biomass continued to increase from the late 1970s to 1990 as warm-water conditions continued and exploitation rates remained less than 10% per year. Thus, since the early 1930s, sardine biomass increased with warm water and low exploitation rates, and decreased with cold water and higher exploitation rates (>20% per year).

DISCUSSION

Sardine analyses prepared for the September 1990 workshop provided a foundation for discussions about the status and management of sardines. The workshop approach offered an effective format for assembling current data from diverse sources and developing timely population estimates needed for management during the initial stages of recovery. Concerns about weaknesses in individual analyses were alleviated by general agreement among the independent lines of evidence.

All of the analyses presented at the workshop indicated a generally increasing trend in sardine bio-

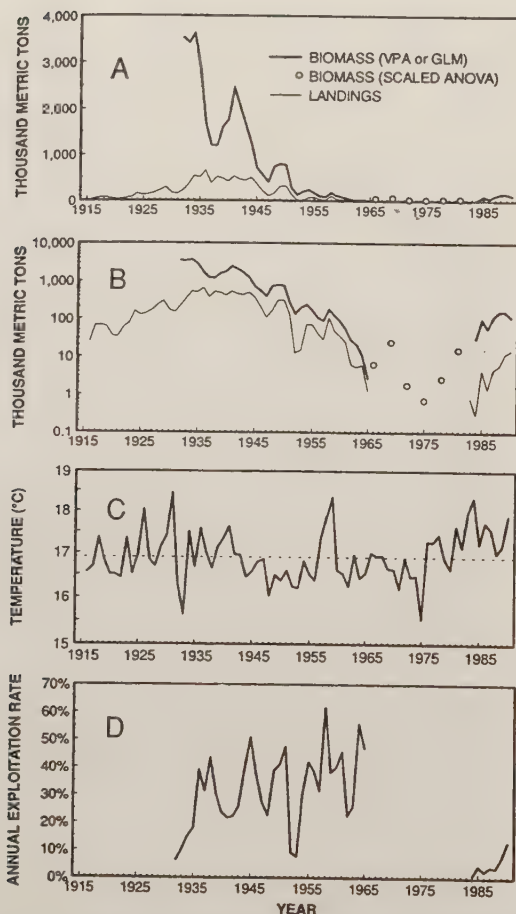


Figure 6. (A,B) Biomass estimates and landings data for Pacific sardines; (C) mean annual sea-surface temperature data from Scripps Pier; and (D) annual exploitation rates for sardines. Biomass estimates for 1932–44 are from VPA analysis by Murphy (1966); estimates for 1945–65 are from VPA analysis by MacCall (1979); estimates for 1966, 1969, 1972, 1975, 1978, and 1983 are scaled ANOVA values from figure 1 and MacCall and Prager (1988), with low-weight years omitted; estimates for 1984–90 are from a general linear model (table 4). Landings data for 1916–49 are from Murphy (1966); data for 1950–65 are from MacCall (1979); and data for 1983–90 are from table 1. Landings data for 1916–65 are for fishing seasons (e.g., the data for 1916 are for landings from June 1916 to May 1917); landings data for 1983–90 are for calendar years. The effects of mixing landings data from calendar years and fishing seasons are insignificant. A crude measure of annual exploitation for sardines in each year was obtained by dividing annual sardine landings (California plus Ensenada) by sardine biomass.

mass from the late 1970s to 1989. The rate of recovery slowed during 1990–91, but there was no indication of year-class failure.

The range of biomass estimates from our analyses was broad, illustrating the uncertainty about current sardine abundance levels. A subjective conclusion

based upon a majority of the data and findings at the workshop was that the 1990 spawning biomass probably fell within the 95% confidence limits of the general linear model analysis, i.e., 60,000–210,000 MT.

The analyses described in this paper were designed to make simultaneous use of a variety of data, although no single assessment used all of the available data. The results we obtained indicate that more completely integrated models (Deriso et al. 1985; Gavaris 1988; Methot 1989) based on fishery-dependent and fishery-independent data will be useful for sardine assessments. We expect that one facet of sardine research will be to develop better population models of this type.

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APPENDIX

TABLE A
Sardine Length-Frequency Data (SL, mm) from Landings at Terminal Island and San Pedro, 1988-1990

Length (mm)	1988							1989						
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
<151	1	—	—	—	—	—	—	4	—	—	—	—	—	—
151-155	—	—	—	1	—	—	—	6	—	3	2	—	—	—
156-160	—	—	—	—	—	1	—	1	—	3	6	—	2	1
161-165	—	—	—	1	—	1	—	2	—	22	12	—	8	3
166-170	—	—	—	3	—	—	1	—	1	17	19	—	7	8
171-175	—	—	—	3	—	3	—	2	—	12	20	—	10	7
176-180	1	2	—	9	—	9	—	4	—	7	16	—	4	3
181-185	3	5	1	5	—	7	—	1	—	11	9	—	7	17
186-190	7	—	1	9	—	10	—	7	—	5	8	—	13	43
191-195	11	—	4	4	—	4	1	17	5	9	4	—	9	63
196-200	29	—	3	14	—	3	—	21	4	16	13	—	7	45
201-205	23	1	16	23	2	5	—	13	5	8	14	1	12	39
206-210	20	—	29	36	5	9	1	26	11	19	12	—	24	28
211-215	19	3	51	46	10	13	3	27	20	25	23	2	20	39
216-220	7	9	39	71	8	21	7	58	33	36	37	—	32	43
221-225	4	16	29	36	5	8	6	39	47	39	46	3	40	28
226-230	—	12	11	31	3	17	5	33	28	29	41	8	17	12
231-235	—	7	3	9	2	14	4	18	27	13	32	5	13	5
236-240	—	7	5	6	—	7	4	11	7	5	26	1	7	4
241-245	—	1	—	1	—	1	1	2	4	1	10	3	3	—
246-250	—	1	2	2	—	—	1	2	3	1	12	2	—	—
251-255	—	—	1	—	—	—	—	1	1	—	3	—	—	—
256-260	—	—	—	—	—	—	—	—	—	—	4	—	—	—
261-265	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	125	64	195	310	35	133	34	295	196	281	369	25	235	388

Length (mm)	1989					1990								Total*
	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
<151	—	—	—	—	—	5	—	—	—	—	—	—	—	10
151-155	—	—	—	—	—	—	—	—	—	—	—	—	—	12
156-160	—	—	—	—	—	1	—	—	—	—	—	—	—	15
161-165	1	—	—	—	—	—	—	—	—	—	—	—	—	1
166-170	2	—	2	—	—	—	—	—	—	—	—	—	—	51
171-175	8	—	6	—	—	—	—	—	—	—	—	—	—	62
176-180	27	14	21	1	5	2	—	1	—	—	—	—	—	72
181-185	46	25	55	3	9	14	2	—	—	—	—	—	—	128
186-190	85	23	118	15	35	39	4	5	6	—	—	—	—	224
191-195	149	47	190	20	46	93	6	21	7	—	—	—	—	436
196-200	177	50	223	30	64	115	19	49	4	—	—	—	—	712
201-205	127	51	101	15	51	108	41	77	13	1	2	2	—	886
206-210	134	37	37	7	17	132	39	131	16	1	5	4	5	751
211-215	173	39	23	4	7	93	40	103	12	2	23	24	12	785
216-220	148	43	23	2	8	85	48	155	14	8	32	42	14	856
221-225	104	36	11	2	4	56	52	118	8	5	57	41	36	1,023
226-230	47	25	4	—	2	36	26	91	10	6	63	47	40	876
231-235	14	15	—	—	—	14	22	32	1	4	48	30	22	644
236-240	6	12	—	—	—	7	9	15	1	6	34	23	17	354
241-245	2	5	—	—	—	1	4	6	2	1	18	10	3	220
246-250	—	1	1	—	—	—	3	2	1	1	6	13	4	79
251-255	—	—	—	—	—	—	—	3	—	—	4	7	1	58
256-260	—	1	—	—	—	—	—	—	—	—	—	—	2	21
261-265	—	—	—	—	—	—	1	—	—	—	—	—	—	7
Total	1,250	424	815	99	248	801	316	809	95	35	292	243	171	8,283

*June 1988-August 1990

TABLE B
 Average Round Weight (g) by Age of Sardines from Landings at Terminal Island and San Pedro, 1988-1990

	Year class											Weighted average*
	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	
1988												
Jun			—	96.0	137.2	163.8	146.0	—	—	—	—	136.6
Jul			—	133.0	194.0	197.7	202.1	175.0	230.0	—	—	194.5
Aug			—	117.3	152.0	166.4	185.9	205.0	218.0	—	—	155.5
Sep			—	105.1	155.4	175.1	188.0	—	—	—	—	157.6
Oct			—	—	146.4	162.2	—	168.0	—	—	—	151.5
Nov			55.0	90.2	153.6	180.3	196.8	201.0	183.0	184.5	—	152.7
Dec			—	—	136.3	146.7	152.0	—	—	—	—	173.9
1989												
Jan		—	110.4	116.2	141.7	161.5	184.4	199.0	—	—	—	154.9
Feb		—	80.5	116.8	173.2	197.7	200.7	203.0	213.0	167.5	—	176.6
Mar		—	69.2	108.0	163.6	170.2	185.1	—	—	—	—	139.9
Apr		—	75.5	104.5	164.5	204.2	217.1	230.8	195.4	197.0	182.0	150.9
May		—	—	149.0	186.5	164.5	192.3	—	—	—	—	181.2
Jun		64.3	98.3	133.6	162.2	164.6	186.6	201.2	—	—	—	149.5
Jul		83.9	106.2	119.8	150.3	158.5	169.2	192.8	—	—	—	132.6
Aug		111.1	111.8	127.9	148.5	156.4	166.0	—	—	—	—	134.5
Sep		—	108.3	133.2	153.4	180.1	185.1	175.4	—	—	—	132.9
Oct		84.8	101.3	116.0	138.4	160.8	138.2	148.1	—	—	—	104.9
Nov		—	108.6	122.3	125.2	—	159.3	—	—	—	—	112.2
Dec		—	103.8	117.9	120.0	153.3	131.4	—	—	—	—	108.1
1990												
Jan	—	89.4	123.4	147.8	158.3	170.2	160.5	147.9	—	—	—	134.2
Feb	—	121.9	130.1	157.8	170.0	168.2	160.2	—	—	—	—	148.1
Mar	—	116.0	134.2	157.4	162.9	165.3	170.4	185.7	192.4	—	—	151.7
Apr	—	110.4	134.8	156.5	167.4	185.8	—	—	—	—	—	148.3
May	—	—	128.4	168.9	183.2	197.9	—	—	—	—	—	171.7
Jun	—	—	163.0	177.7	184.5	197.8	190.5	210.4	—	—	—	180.9
Jul	—	—	156.3	171.6	176.1	185.6	189.3	200.9	214.3	—	—	173.0
Aug	60.5	—	162.1	163.7	172.7	176.4	189.3	—	—	—	—	166.5

*All ages combined

TABLE C
 Age Composition (Number of Fish) of Sardines from Landings at Terminal Island and San Pedro, 1988-1990

	Year class											Sample size
	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	
1988												
Jun			1	2	99	6	2	—	—	—	—	110
Jul			—	6	9	24	17	4	1	—	—	61
Aug			—	6	142	12	10	2	1	—	—	173
Sep			3	30	206	34	20	—	—	—	—	293
Oct			—	—	28	5	—	1	—	—	—	34
Nov			1	29	64	16	15	3	1	2	—	131
Dec			—	—	4	3	1	—	—	—	—	8
1989												
Jan		—	15	25	73	15	8	3	—	—	—	139
Feb		—	2	4	142	22	11	6	1	2	—	190
Mar		—	63	38	140	16	15	—	—	—	—	272
Apr		—	41	13	58	17	24	9	5	1	1	169
May		—	—	3	16	2	4	—	—	—	—	25
Jun		7	18	55	62	7	8	1	1	—	—	159
Jul		7	56	178	117	20	7	2	—	—	—	387
Aug		5	51	184	197	45	10	—	—	—	—	492
Sep		—	143	112	75	19	5	2	—	—	—	356
Oct		7	670	81	30	4	1	1	—	—	—	794
Nov		—	75	19	3	—	1	—	—	—	—	98
Dec		—	173	60	6	1	1	—	—	—	—	241
1990												
Jan	—	48	386	218	78	13	15	1	—	—	—	759
Feb	—	1	132	120	43	10	5	—	—	—	—	311
Mar	—	5	298	285	127	47	23	5	1	—	—	791
Apr	—	7	44	25	11	8	—	—	—	—	—	95
May	—	—	4	16	12	3	—	—	—	—	—	35
Jun	—	—	56	84	105	27	14	5	—	—	—	291
Jul	—	—	48	79	76	22	12	5	1	—	—	243
Aug	5	7	56	45	40	10	6	—	—	—	—	169
Total	5	94	2,336	1,717	1,963	408	235	50	12	5	1	6,826

Status of Bocaccio
in the Conception/Monterey/Eureka INPFC Areas
in 1992 and Recommendations for Management in 1993.

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Abstract

Analyses using the stock synthesis model indicated that biomass and spawning stock size of the Conception/Monterey/Eureka INPFC areas' bocaccio had declined substantially since 1980. This qualitative result was in agreement with trends in both recreational catch/effort and a research survey index of abundance. As was the case in the last assessment of bocaccio, we had difficulty in ascertaining the absolute biomass level, and the extent to which fishing, along with a reduction in recruitment rates, contributed to the estimated decline. Fishing mortality rates appear to have fallen substantially from 1990 to 1991, following the imposition of trip limits, and were estimated to be below $F_{35\%}$ levels. Based on average estimated 1980-1990 recruitment rates, 1991 landings/catch (about 1700 MT) were estimated to be near the equilibrium $F_{35\%}$ rate. Nevertheless, under continued 1991 landing levels, the bocaccio stock was projected to continue to decline; under some reasonable scenarios the spawning stock was forecast to fall below 20% of 1980 levels within the next few years. The continued forecast decline from 1980 levels occurred because the forecast recruitment rate (the average of 1980-1990 estimated recruitment) was substantially less than the recruitment rate that produced the initial 1980 stock. If recent recruitment is indeed substantially below virgin levels, then the spawning stock may well fall below 20% of its virgin level. If landings were held at the current harvest guideline of 1100 MT, our forecasts were for increases in biomass by 1994. We recommend this conservative approach both because of the apparent decline in recruitment, and because we may have underestimated 1991 fishing mortality rates since discard was not accounted for in our analyses, and could have increased following the imposition of trip limits in 1991.

Introduction

This report presents an analysis of data on bocaccio (*Sebastes paucispinis*) from the Conception, Monterey, and Eureka INPFC areas combined over the period 1980-1991, with a view toward assessing the current status of the stock. Included is a recommendation for management in 1993.

Bocaccio is a viviparous demersal rockfish which is frequently landed together with chilipepper rockfish (*S. goodei*). Among rockfish, bocaccio are noted for their rapid growth, large adult size and high variation in year-class strength. This species reaches a maximum total length (tl) of approximately 90 cm. Past assessments indicate that bocaccio reach 50% recruitment to the trawl fishery at about age 2 and tl 40 cm (Bence and Hightower 1990), but females do not reach 50% maturity until 48 cm in length. Some individuals older than 30 years have been captured, but the bulk of the population appears to be less than 15 years in age.

Although bocaccio are found from Baja California to north of the US/Canadian border, there appears to be a break in its distribution in southern Oregon, near the boundary between the Eureka and Columbia INPFC areas (Bence and Hightower 1990). Consequently, we confined our assessment to the Conception/Monterey/Eureka areas.

This document updates earlier assessments prepared by NMFS and CDF&G. The most recent full stock assessment of bocaccio was done in 1990 (Bence and Hightower, 1990). That assessment was based on the separable Stock Synthesis model (Methot 1989 & 1990), and explicitly included the trawl, set-net and recreational fisheries. Bence (1991) provided updated length composition data which appeared to be consistent with the earlier assessment. The 1990 assessment for bocaccio strongly indicated that the biomass and spawning stock size had declined substantially over the 1978-1989 period. Best estimates of stock size suggested that the biomass had fallen to less than 20% (seven to 14 thousand MT) of its 1978 level by 1990. Both the NMFS triennial survey data, and recreational effort data provided evidence for this decline. It was also concluded that a significant fraction of the decline was due to poor recruitment since 1978. Bence and Hightower (1990) emphasized that the available data were not sufficient to firmly fix current fishing mortality rate or the extent to which fishing

contributed to the observed decline in bocaccio abundance. Because of the apparent decline in recruitment, a conservative management approach was recommended. Based on that assessment, an ABC of 800 MT and a harvest guideline of 1100 MT were adopted for the Conception/Monterey/Eureka areas combined, representing substantial reductions from the previous ABC of 6100 MT for only the combined Monterey and Conception areas. In an attempt to reduce the landings of bocaccio (and other rockfish), in 1991 a trip limit was set for the area south of Coos Bay, Oregon. The limit was 25,000 lbs. for the Sebastes complex, to not include more than 5000 lbs. of bocaccio.

Our use of the stock synthesis model in this assessment was similar to its use by Bence and Hightower (1990). The most significant changes were (1) a revision of the natural mortality rate downward to 0.20 from 0.25 based on observed maximum ages, (2) the allowance of time-dependence in the selectivity of the trawl fishery, (3) the inclusion of length-at-age data for the trawl fishery, (4) the inclusion of the hook-and-line / long-line fishery, which was not accounted for at all in the previous assessment, and (5) changes in the landings data used (see Attachment 1). (Note that we include in the hook-and-line / longline fishery all commercial landings by hook - for brevity we sometimes refer to this fishery as hook-and-line or just "hook".)

Methods

The stock synthesis model was the analytical tool we used to assess the current status of the stocks. We used the length-based version of the model termed "stage-2" by Methot (1989). The rationale for our use of this variant of the synthesis model was presented in Bence and Hightower (1990).

The model was fitted by maximizing the weighted log likelihoods attributable to each of the data sources. These included length and age composition observations, length at age data, recreational effort data, and triennial survey data, and penalty functions (see below). The age and length composition data were assumed to demonstrate a "multinomial like" variance pattern, but we set effective sample sizes to 200 whenever more than 200 fish were actually measured or aged (e.g. Methot 1990, Fournier and Archibald 1982). We used a smaller effective sample size for the 1980, 1983 and 1986 triennial survey length composition data because the 1980-1986 length compositions were based on only 9-18 samples containing bocaccio (see below). We also reduced the emphasis for all the triennial survey length composition data to 0.25 from the emphasis of 1 used for other data sources. We did this because of other concerns we had about the length composition data for the triennial survey: (1) during the 1980 and 1983 surveys only samples with 10 or more bocaccio were measured for lengths, and (2) the indicated relative strength of year classes were inconsistent over time and with other samples.

Available Data

The analysis made use of data from the trawl, set-net, hook-and-line / longline, and recreational fisheries, and from the NMFS triennial trawl surveys. Landing estimates from the commercial fisheries (Tables 1-3) were used together with catch estimates for the recreational fishery for 1980-1989 (Table 4) obtained in a database from John Witzig (NMFS, Washington, DC.) Recreational catch in 1990 and 1991 was assumed to be the average of the estimated values reported for 1987-1989.

We included composition data on ages 1-21+ and on lengths in 2 cm total length bins from 20 to 56 cm, and in 4 cm bins up to an 80+ cm category. These data were separate by sex except for the recreational fishery, and for the hook-and-line / longline fishery in 1990. The length (Fig. 1) and age compositions (Fig. 2) for the trawl fishery were obtained from "CSUM" expansions (see Attachment 1). For the trawl fishery, length compositions were available for each year, while age compositions were available only for 1980-1984. Similar "CSUM" length compositions were provided by CDF&G for the set-net fishery for 1986-1991 (Fig. 3). These expansions for set net did not account for all reported landings, but we believe they are reasonable estimates of the length

composition for this fishery. Similar expansions were not available for the other gear types. For hook and line / longline (Fig. 4) and the recreational fishery (Fig. 5), we generated length compositions by simply pooling the available samples for a given year (separately by sex when appropriate). For hook and line / longline we chose to use raw length compositions both because of the sparse sampling and because up-to-date landing data were not available at the time the length compositions were calculated. Recreational length data were only available in raw form (not tied to stratified landing values). Sufficient data were available to generate length compositions for 1986-1991 for the hook-and-line fishery and for 1980-1989 for the recreational fishery. Too few age data were available to generate age compositions for any years for the non-trawl fisheries.

We also used length composition data for the triennial trawl survey (Fig. 6). These length compositions were generated by AFSC as swept area estimates of the numbers at size based on a stratified sampling plan. They were, however, based on relatively few samples each year. There were 14, 9, 18, and 40 samples with length composition data for bocaccio in the respective 1980, 1983, 1986, and 1989 surveys. For this data set, we set the effective sample sizes as $200 \times p$, where p was the ratio of the number of samples contributing length information in a given year to the number contributing information for the 1989 survey (40). For reasons discussed above, we suspect that this still over-estimated the actual effective sample size.

For the trawl fishery, we also included length-at-age data for 1980-1984 along with the sample sizes used to calculate these values. Auxiliary data included effort data for the recreational fishery and an index of abundance for the NMFS triennial bottom trawl survey. Our past analyses indicated that the swept area estimate of abundance from the triennial survey was highly sensitive to a few very large tows. Therefore, after Bence and Hightower (1990), we used winsorized CPUE (Kg/tow) as an index of abundance (Table 5). For the recreational fishery, the effort values we used were weighted sums of the reported numbers of trips. We calculated the average weight of bocaccio over cells (i.e. regions, areas, and waves (bimonthly periods)). These average values were then used to weight trips from different fishing modes (e.g. shore fishing versus party boats). In Table 6 we report the ratio of estimated catch to these effort values as an index of relative abundance, but we stress that in the synthesis runs these auxiliary data were input as effort estimates.

Implementation of the Synthesis Model

Our implementation covered years 1980-1991, and recognized ages classes 1-21+. The parameters we fixed (i.e. assumed or estimated outside of the synthesis model), and the parameters estimated by synthesis are listed in Table 7.

Natural mortality was assumed constant over time and independent of age, and was fixed at 0.20 in our main set of runs. We revised the natural mortality rate downward from 0.25 used by Bence and Hightower (1990), to be more consistent with the maximum observed age in trawl data of 36 yr. By itself, a maximum age of 36 implies a natural mortality rate under 0.15 (Hoenig 1983), but we chose a value of 0.20, (a) because of the relatively high Brody growth coefficient (k) (see Henry 1986), and because widow rockfish reach greater maximum ages than bocaccio, but catch curve analyses of relatively unexploited stocks of this species indicate a natural mortality rate on the order of 0.15-0.2 (Hightower and Lenarz 1986).

Selectivities of all four fisheries and the survey were modeled as the double logistic form, with the ascending function assumed to be the same for both sexes, but with the descending function allowed to differ between the sexes. The use of the same ascending function for both sexes was based on runs done for the 1990 assessment, where estimated ascending functions for the two sexes were very similar (Bence and Hightower 1990). In general, each selectivity function required that nine parameters be estimated within the synthesis runs: (1) the selectivity at 20 cm, (2-3) the slope and size of inflection for the ascending component of the function, (4-7) the slope and size of inflection for the descending component of the function for each sex, and (8-9) and the selectivity

at length 80 cm for each sex. We were able to reduce the number of estimated parameters by fixing the selectivity at 20 cm to near zero for the trawl, set-net and hook-and-line fisheries because these did not catch fish that small. Calculated derivatives for the inflection size of the downward components of the selectivity functions were sometimes ill-behaved, presumably because when the slope parameters approach zero the value of the inflection size becomes irrelevant to the likelihood. To make these derivatives well defined we introduced penalty functions which contributed to the likelihood when the estimated inflection sizes for the downward components deviated from a value of 50 cm. These penalty functions were given an emphasis of 10 and CV's of 20% around the prior value of 50 cm. The penalty functions allowed the estimated values to change from 50 cm when this was required to fit the data, and solved the numerical problem when this was not the case.

There were also numerical problems associated with estimating the triennial selectivity function, as no given selectivity pattern fit all the triennial length composition data well. When free, the parameter for selectivity at 80 cm usually increased toward 1. Given these patterns and the numerical problem, we fixed this parameter close to 1. When freed up again after the model converged to a solution, the parameter generally stayed at this value (an upper bound of allowed values).

Bence and Hightower (1990) argued and presented analyses indicating that the trawl fishery might be targeting on strong year-classes of bocaccio, leading to a time-dependence in selectivity. In preliminary runs we again found evidence for this. We therefore allowed the selectivity of the trawl fishery to be time-dependent, by letting the inflection size of the ascending function be year-specific. By adding 11 additional parameters, the total likelihood of our fit increased by nearly 200 units and a pattern in the trawl residuals was removed. Figure 7 shows that the estimated value of the ascending inflection size fell quite sharply in 1986, when the relatively strong 1984 year class entered the fishery. As a consequence, fish under 40 cm in total length were nearly fully recruited that year, but in other years fish of the same size had very low selectivity (Fig 7).

We assumed that the trawl ages were measured with error, and fixed the proportion agreement between two readers at 0.75 and 0.1 for ages 1 and 21 respectively, with an assumed linear decline with age. These values were calculated from values estimated by the synthesis model for the 1990 assessment. In that assessment, age-composition data for 1978 and 1979 were also used. This allowed ageing error parameters to be well estimated as the strong 1977 year class aged, and coded ages "smeared". With only the 1980-1984 age compositions used here, the ageing error could not be well estimated internally by the synthesis model.

Males and females each followed separate von Bertalanffy growth equations, and all parameters for the growth equations were estimated within the synthesis runs. This differs from the 1990 assessment, where the length at age 1 was fixed based on observed mean length at age seen in the 1977 triennial survey. We have concluded that fixing the length at age in this way gives too much weight to a single survey done prior to the time period covered by the assessment. Following Bence and Hightower (1990), CV's in length at age were fixed at values based on a regression of observed CV in length at age (from trawl data) versus mean length at age for females and at the mean CV in length at age averaged over all ages for males (since there was no significant regression or obvious pattern for males).

The initial age composition for ages 1-15+ were estimated as parameters, except for the initial numbers at age 3 (the 1977 year class). Thus the model recognized the 15+ class in 1980, the 16+ category in 1981, and so on, until all 21 age classes are present. In our runs, we fixed the strength of the 1977 year class by setting the initial numbers at age 3 at values ranging from 15 to 60 million fish.

Results

Qualitative patterns in the data

Landings/catch estimates are summarized in Tables 1-4. The estimates of commercial landings were revised and extended from those used in the 1990 assessment, and landing estimates for the hook-and-line / longline fishery from 1980-1991, and the set-net fishery prior to 1986 were added. All nominal landings by gear and INPFC area were adjusted for unknown gear landings and landings from Santa Barbara and further south. Details of how the revised landing estimates were obtained are included in Attachment 1.

Historically, bocaccio has been an important mainstay of the California trawl rockfish fishery (Lenarz 1986). In 1985, trawl landings of bocaccio fell sharply from around 4000 MT to just over 1000 MT, as the large 1977 year class left the fishery, and remained at this lower level through 1990 (Table 1). In 1991, trawl landings of bocaccio dropped from over 1400 MT to just below 700 MT. During 1985-1990, landings from set-net (Table 2) and hook-and-line (Table 3) fisheries did not fall, most likely due to increased effort. Set-net landings of bocaccio have varied from 70 to nearly 1200 MT since 1980, with peak landings occurring during 1985-1987 (Table 2). As with trawl, bocaccio set-net landings fell from 1990 to 1991. Hook-and-line / longline landings have varied from less than 20 MT in 1980 to about 500 MT since 1989 (Table 3). Recreational catch reached nearly 2000 MT in 1980 and exceeded 1000 MT in 1982 (Table 4). In the last three years with available estimates (1987-1989), recreational catch was about 200 MT (Table 4).

Most commercial landings for all gear types have come from the Monterey area, although the Conception area set-net and hook-and-line / longline landings exceeded the Monterey landings during the early 1980's. There were essentially no set-net landings in the Eureka area, and hook-and-line / longline landings were relatively low there.

Length and age composition data showed clear indications of three dominant year classes. The strong 1977 year class can be followed in the 1980-1985 trawl length compositions (Fig. 1), and the trawl age compositions for 1980-1984 (Fig. 2). The growth of the 1977 year class can also be tracked in the triennial survey length compositions (Fig. 6). A relatively strong 1984 year class first showed up in the trawl fishery length composition data in 1985, and can be followed as it grows and recruits more fully to the fishery (Fig. 1). This same year class did not create a distinct mode in the set-net fishery until 1987 (Fig. 3), appeared to be evident, but only weakly in the 1986 hook-and-line length composition (Fig. 4), but could be easily detected in the recreational length compositions as 0+'s in 1980 (Fig. 5). This year class was evident in the 1986 triennial survey as small two year old fish, but did not form a distinct mode in the 1989 survey, where 1+ fish from the 1988 year class appeared to dominate (Fig. 6). Like the 1984 year class, the 1988 year class was quite evident as 0+'s in the recreational length composition (Fig. 5), and was evident in the trawl length compositions as two-year-olds (Fig. 1).

The clear pattern in both sets of auxiliary data is for a decline in relative abundance over time. Our winsorized index of CPUE for the triennial trawl survey is reported in Table 5. In Table 6 we report catch/effort for the recreational fishery. These numbers were simply the estimated catch divided by our effort estimates calculated for use in our synthesis runs.

Synthesis fits

In preliminary runs, we found that the model could not discern the best absolute biomass level over a substantial range of levels. We therefore fixed the strength of the 1977 year class by fixing the initial numbers at age-3 (I3) at 1.5, 2.25, 3.0 and 6.0 (in 10's of millions). This was akin to fixing the terminal F in a cohort or VPA analysis. The absolute change in likelihood over this wide range of conditions was not great, but the total weighted likelihoods for the high and low I3 levels indicated somewhat poorer fits (Table 8).

There was no consistent pattern that a given level of I3 provided the best fit to all sources of data. The likelihoods for the trawl age composition data indicated somewhat better fits at the two higher I3 levels, but the trawl size composition likelihoods were roughly equal for all I3's (with the nominally best fit at I3=2.25). The likelihoods indicated that the length-at-age data were fit better as I3 declined. The likelihoods were about equal at the three lower I3 levels for the set-net size-composition data, with a somewhat better fit indicated at I3=6.0. The fit to the recreational size composition data degraded as I3 increased, but the likelihoods were about equal for I3=1.5 and I3=2.25. The fit to the hook-and-line size composition data degraded as I3 increased, but not substantially. The likelihood for the triennial survey index was highest for the lowest I3 and the fit degraded as I3 increased. The range of variation in these likelihoods was not great. The likelihoods for the effort data were roughly equal for all I3, although the values at I3=3 and I3=2.25 were slightly higher than at the extremes.

The model was able to match the qualitative pattern of a decline in biomass, apparent in the auxiliary data, for all values of I3 examined. The match between observed and predicted (by synthesis) triennial index values are given in Fig. 8. None of the fits were especially good because the model was not able to emulate the sharp drop in the observed index from 1986 to 1989. The lower I3 values produced "better" fits because they matched the overall drop in the index from 1980 to 1989. Catch/effort for the recreational survey dropped over time and was well fit by all the synthesis runs (Fig. 9). It is clear from this figure that the nominal differences in effort likelihoods among the cases were insignificant.

Based on the better overall fits, we chose the I3=2.25 and I3=3 runs as our more likely solutions. We ruled out the I3=6 case because we considered implausible the very low fishing mortality rates, the very high initial biomass and the implied very large drop in average recruitment. We decided against the I3=1.5 run based on its lower likelihood. We stress, however, that the entire range of variation in likelihoods was not large, and solely based on the synthesis fits none of the cases we examined can clearly be dismissed.

The fits of our preferred two runs were similar, and we illustrate the fit of the model to all the length, age, and length-at-age only for the I3=2.25 case. Table 9 gives the estimated (by synthesis) and observed mean lengths and ages for each of the composition samples, together with the estimated and observed proportion female. Excluding the triennial trawl length composition data, there was generally good agreement between estimated and observed values, with several notable exceptions. The two most notable such discrepancies were for the 1984 trawl fishery age composition data (both sexes), and for the 1990 hook length composition data (sexes pooled). The lack of fit for the 1984 age data could be due to a change in age (rather than size) dependent selectivity in response to the strong 1977 year class. We have no mechanistic explanation for the generally small size of fish in the 1990 hook-and-line data. Given that the mean length observed in 1990 was smaller than the lowest mean length observed in other years for either sex, and much lower than both 1989 and 1991 values, we suspect that the discrepancy is due to sampling error. The various problems with fitting the triennial data were discussed above. Our conclusion is that these data have high levels of observation error. We suspect that this might be due to clustering of like-size fish within samples, combined with the small sample sizes.

The fit to the proportion female was much poorer, and the observed proportion female was much more variable over time, than were the values estimated by synthesis. This could be due to time-dependent changes in selectivity that were not captured in the model, or to clustering of sexes in the samples leading to large errors in observed sex ratio. It is clear that the variations do not indicate similar variation in the sex ratio of the underlying population because the fluctuations are not concordant for the different gear types.

The observed and predicted lengths-at-age, as a function of age, are shown separately by sex in Fig. 10, again for the I3=2.25 run. In general there was a fairly good fit, but the model did tend to underestimate the length-at-age for the oldest fish slightly, especially for males.

All the estimated parameters for our two preferred runs are in Table 7. The estimated selectivity patterns were similar for our two preferred runs, and these patterns for the hook, recreational and set-net fisheries are illustrated for the $I3=2.25$ case in Fig. 11, (see Fig. 7 for trawl) and for both of the preferred $I3$ values and all fisheries in Tables 10 and 11. Full selectivity was estimated at all sizes for the triennial survey and is not illustrated.

Selectivity for each of the fisheries was estimated as dome shaped, with peak selectivity for females exceeding peak selectivity for males, and selectivity for males beginning to descend at a smaller size than for females (Figs. 7 and 11). There was also a suggestion that the selectivity for very large males by the hook and recreational fishery may be higher than for females. This latter pattern may not be especially meaningful since very few males reach these sizes. The recreational fishery has the broadest estimated selectivity function, and estimated selectivity for small fish was stronger than for any of the other fisheries. In some years the estimated selectivity of the trawl fishery for small fish was substantially higher than that of the hook or set-net fisheries, and on average, the estimated length of peak selectivity for this fishery was less than for the other commercial fisheries (Figs. 7 and 11). However, the trawl fishery also had higher estimated selectivities for the largest fish than any other fishery. The set-net fishery had the narrowest estimated selectivity pattern, with very low selectivity below 40 cm or above 60 (males) or 65 cm (females) (Fig. 11). The hook fishery had an estimated peak selectivity at a larger size than in any other fishery (near 60 cm), but the estimated selectivity pattern also had a long tail to the left, indicating significant selection for smaller fish also (Fig. 11).

The dynamics of the fish stock and fishery implied by the estimated parameters are illustrated in plots of recruitment (Fig. 12), biomass and spawning stock (Fig. 13) and fishing mortality rate (Fig. 14) for each run. In addition, numbers-at-age over time, by sex, are given for the $I=2.25$ (Table 12) and $I3=3$ (Table 13) runs.

The model estimated the 1979, 1983, 1984, 1987 and 1988 year classes as being relatively strong (Fig. 12). The pattern of "double" strong year classes resulted, we suspect, from the model misclassifying the age of some of the larger fish from the 1984 and 1988 year classes. There was some evidence that strong year classes of bocaccio tended to recruit earlier and possibly grow faster, thus leading to larger size at age. We were not able to resolve this possible problem in the absence of recent age composition data. This "splitting" of year classes should not have seriously affected this assessment, but caution should be exercised in using the time series of estimated recruitments in other contexts (e.g. in spawner-recruit relationships).

The $I3=6$ run estimated substantially higher recruitment rates than the other runs (Fig. 12). In contrast, the differences in average estimated recruitment for the $I3=1.5$ through $I3=3$ runs were much less than the differences in the fixed $I3$ levels. All the runs estimated the 1987/1988 year class to be about as strong as the 1983/1984 year class.

All runs estimated that biomass and spawning stock declined substantially from 1980 through 1991, but the extent of the decline was increased as $I3$ decreased (Fig. 13). Estimated 1991 biomass levels range from 22 to 42 percent of 1980 levels, and 1991 estimated spawning stock was at 18 to 44 percent of 1980 levels (Fig. 13, Table 15).

Temporal patterns in estimated fishing mortality rates differ substantially among the fisheries because of the different patterns in landings (Fig. 14, Tables 1-4). Trawl fishing mortality peaked in 1984, fell sharply in 1985, and for all runs except the $I3=6$ case gradually increased through 1990, then fell in 1991 as trip limit regulations came into play (Fig. 14). For all cases, set-net fishing mortality increased dramatically from 1980 through 1986, then declined somewhat, but still remained at much higher levels than was evident at the beginning of the 1980's (Fig. 14). There appeared to be a modest drop in fishing mortality from 1990 to 1991. For all cases, recreational fishing mortality was estimated as being highly variable over time, perhaps because of large observational error associated with the estimated landings (Fig. 14). Overall, estimated fishing mortality rate for this fishery was less in recent years than

the average seen in the early to mid-1980's. For all runs, the hook-and-line fishery showed a dramatic increase in estimated fishing mortality from 1986 through 1990, and only a slight drop off in 1991 (Fig. 14).

Such a wide range of cases were able to predict that biomass and spawning stock declined substantially from 1980 to 1991 because they traded off changes in recruitment levels and fishing mortality rates. Average recruitment for 1971-1979 (based on estimated initial numbers at age), for 1980-1990 and for 1971-1990 are presented in Table 14. For all cases, recent (1980-1990) average estimated recruitment was lower than for the early period (1971-1979). Thus, in all cases a decline in recruitment from the rate that produced the initial stock in 1980, in addition to direct effects of fishing, was required to fit the data. Of special interest here is that the early recruitment became proportionally greater than recent recruitment as I_3 increased from 1.5 to 6. Thus, when the fishing mortality rate was estimated to be lower, a greater drop in average recruitment from historical levels was required to explain the observed patterns in the data.

Yield Calculations and Forecasts

The various factors used in our yield calculations are in Table 16. We calculated $F_{35\%}$, $F_{20\%}$, equilibrium yield (MT) and equilibrium spawning stock size (in billions of eggs) under the assumption that the ratio of the fishing mortality rates for the various fisheries averaged over 1989-1991 would be experienced in the future. Selectivity (converted to an age-specific form), and weight-at-age for each fishery used in these calculations were based on the $I_3=2.25$ run. Spawning capacity of an individual female of a given age was measured in expected numbers of eggs carried, and was the product of the proportion of females mature at that age, the weight at age, and the eggs/unit mass carried by a female of that age. Total spawning stock size is then calculated as the sum of spawning capacity over all individuals.

Fig. 15 summarizes the results of our equilibrium yield calculations. Equilibrium spawning stock, as a proportion of the unfished equilibrium, was plotted against trawl F (at selectivity of 1). Because this curve assumed that recruitment rate was constant at all fishing rates and stock sizes, it was equivalent to one for spawning stock per recruit, but started at 1 for $F=0$ and declined as F increased. We also plotted the equilibrium spawning stock as a proportion of the equilibrium "virgin" spawning stock size. In this case, the equilibrium virgin spawning stock was based on an assumed recruitment equal to the 1971-1990 estimated average, but we calculated the equilibrium stock size using the estimated average 1980-1990 recruitment. Because the estimated average 1980-1990 recruitment was less than the 1971-1990 average, these plots started below 1.0 for $F=0$. Also, since the ratio of 1980-1990 average recruitment to 1971-1990 average recruitment differed between the $I_3=2.25$ and $I_3=3.0$ run, these curves differed slightly for the two runs.

Equilibrium yield (MT) is also shown in Fig. 15 for the $I_3=2.25$ and $I_3=3$ cases. At an F of 0.105 the spawning stock fell to 35% of the unfished level ($F_{35\%}$), and at an F of 0.175 the spawning stock fell to 20% of the unfished level ($F_{20\%}$). The corresponding yields were 1680 and 2000 MT ($I_3=2.25$) or 1860 and 2230 ($I_3=3$) respectively. Note, however, that the equilibrium spawning stock sizes at $F_{35\%}$ and $F_{20\%}$ were substantially below 35 and 20% (respectively) of the "virgin" spawning stock, based on the estimated average 1971-1990 recruitment (Fig. 15).

Because the 1980 spawning stock was a product of higher recruitment in earlier years, we should expect that given the lower recent estimated recruitment rates, the spawning stock will fall below 35% of the 1980 level, even when F is at or even below $F_{35\%}$. This was evident in our forecasts of stock size based on 1991 landings in 1992-1995, and assumed recruitment equal to the estimated 1980-1990 average (Table 16). For both the $I_3=2.25$ and $I_3=3.0$ cases, biomass and spawning stock continued to decrease through the beginning of 1996 (although stock sizes and F 's appear to be stabilizing by that time). Spawning stock in 1996 was projected to be 18 ($I_3=2.25$) or 23% ($I_3=3$) of the 1980 estimate, even though $F_{35\%}$ was never exceeded. If we assumed that total catch would be at the

current harvest guideline of 1100 MT, stock biomass was forecast to begin increasing by the beginning of 1994 in both our preferred runs, and spawning stock was projected to begin increasing by the beginning of 1996 for the I3=2.25 run, but not for the I3=3 run (Table 18).

Based on the above analysis we recommend that the current harvest guideline of 1100 MT be retained. With this level of harvest our best estimate is that the expected stock biomass and spawning capacity should remain near its current level. Although the trip limit regulations imposed in 1991 have caused estimated F 's for 1991 to fall well below $F_{20\%}$, and even below $F_{35\%}$, current levels of harvest, which exceed the harvest guideline, should be expected to cause further declines in stock size. Given the evidence for the decline in recruitment rates since 1980, we recommend the more conservative approach implied by the harvest guideline. We stress that when interpreting the above forecasts, the highly variable and unpredictable recruitment in this species should be taken into account. The actual stock trajectory could deviate greatly from its expected value.

Discussion

Under all conditions we considered, estimated biomass and spawning stock declined substantially from 1980 through 1991. As we let the initial numbers at age-3 double, from 15 to 30 million, estimated 1980 biomass only increased from 57,000 to 72,000 MT, and 1991 biomass varied from 13,000 to 22,000 MT. A further doubling in initial numbers at age-3, however, more than doubled both initial and 1991 biomass, but we consider this lightly fished scenario implausible. These results are qualitatively consistent with the 1990 assessment of Bence and Hightower, but our ending biomass estimates are more optimistic (the I=2.25 case is close to the more optimistic of the preferred runs from 1990). Differences are due to the combination of revised landings, a lowered estimate of natural mortality, the use of additional data, and changes to the assessment model, particularly the allowance of time-dependent selectivity.

Even with the more optimistic scenario reported here, the reduction in landings due to the imposition of trip limits in 1991 was needed to keep the estimated fishing mortality substantially below the $F_{20\%}$ level (a possible reference point for overfishing). Furthermore, under current harvesting rates, although fishing mortality is estimated to be below $F_{35\%}$, the expected stock biomass and spawning capacity is projected to decline further, and possibly fall to less than 20% of the levels seen in 1980. This is possible because the initial stock in 1980 appears to have resulted from substantially higher recruitment rates than have been experienced since 1980.

Even though our estimate of current stock status is more optimistic than that of Bence and Hightower (1990), our estimated equilibrium yields at $F_{35\%}$ (1680-1860 MT) are substantially below the $F_{35\%}$ equilibrium yields reported by them (2400-3000 MT). The $F_{35\%}$ rate calculated here is virtually identical to that calculated for the 1990 assessment (after correcting for the fact that they reported F in terms of the trawl fishery on age-5 females and we report in terms of full selectivity for the trawl fishery). The difference in estimated equilibrium yields stems from the fact that they used average 1978-1989 recruitment in their calculations, and this includes the value for the strong 1977 year-class. Although such a strong year class is possible, given the lower recruitments seen since 1980, it is not prudent to count on such an event.

We recommended a conservative approach because, like Bence and Hightower (1990), we estimated that recruitment in recent years had been substantially below the levels seen prior to 1980. If recent lower recruitment is not typical of virgin conditions, then the current biomass could be at or below 20% of virgin levels. If catch continues at the 1991 estimated landings/catch level, on the order of 1700 MT, our forecast is for continued declines in stock biomass and spawning capacity through 1996. Catches on the order of 1100 MT, equal to the current harvest guideline, led to forecast increases in stock biomass by the beginning of 1994. Consequently, we recommend harvesting at the current harvest guideline. A second reason for a conservative approach is that all our analyses have equated landings with catch. If the imposition of trip limits in 1991 led

to increased discarding, then we have over-estimated the decline in fishing mortality rates from 1990 to 1991.

Bence and Hightower (1990) noted two major data gaps associated with their assessment of bocaccio. The first having to do with the lack of set-net landing estimates prior to 1986, and the second being the absence of age-compositions after 1984. The first of these gaps has been filled, together with other improvements and additions to our landing estimates. We believe, however, that as Bence and Hightower forecast, the absence of age data after 1984 is making the assignment of year-class strength more difficult. We recommend, as they did, that any future aging work include a comparison of surface aging (the method used for the 1980-1984 samples) with any new method (such as break-and-burn) that is used. It also seems possible that periodic age-composition data (e.g. every three years) would be adequate for use in assessing the status of the bocaccio fishery.

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Table 1. Estimated trawl landings (MT) of bocaccio for the Conception (C), Monterey (M), and Eureka (E) INPFC areas.

YEAR	C	M	E	TOTAL
1980	938	2632	169	3739
1981	633	2498	1697	4828
1982	830	2909	554	4292
1983	593	3069	645	4307
1984	353	3688	399	4440
1985	100	992	229	1321
1986	127	895	112	1134
1987	206	1031	112	1349
1988	196	983	98	1277
1989	174	1005	124	1303
1990	257	983	178	1418
1991	130	521	48	699

Table 2. Estimated set-net landings of bocaccio (MT) for the Conception (C), Monterey (M), and Eureka (E) INPFC areas.

YEAR	C	M	E	TOTAL
1980	66	8	0	74
1981	203	27	0	230
1982	117	67	0	184
1983	176	291	0	468
1984	187	182	0	369
1985	240	431	0	671
1986	362	781	0	1143
1987	374	499	1	873
1988	221	340	0	561
1989	134	425	0	559
1990	165	359	0	524
1991	122	271	0	393

Table 3. Estimated hook caught landings of bocaccio (MT) for the Conception (C), Monterey (M), and Eureka (E) INPFC areas.

YEAR	C	M	E	TOTAL
1980	85	53	28	166
1981	17	0	0	18
1982	91	19	28	138
1983	110	53	13	176
1984	96	28	1	124
1985	37	34	13	84
1986	78	170	30	279
1987	55	193	32	281
1988	99	213	41	353
1989	130	263	57	450
1990	107	308	73	488
1991	117	255	50	422

Table 4. Estimated recreational catch of bocaccio and for Southern and Northern California (MT).

Year	S. Cal.	N. Cal.	Total
1980	1749	191	1940
1981	423	192	615
1982	1143	356	1499
1983	265	300	565
1984	170	67	237
1985	329	64	393
1986	413	162	575
1987	86	104	190
1988	117	52	169
1989	169	86	255

Table 5. Triennial index of abundance and standard error of index. This index was calculated as a weighted average of winsorized strata means (deep and shallow). After Bence and Hightower (1990).

Year	Index	SE
1980	3.24	0.65
1983	2.64	0.78
1986	1.69	0.56
1989	0.58	0.14

Table 6. Catch/effort (see text) for the recreational fishery. * indicates years index was not included in synthesis runs because index was heavily influenced by recruitment of 0+ fish, which were not included in the model.

Year	CPUE
1980	1.20
1981	0.73
1982	0.99
1983	0.58
1984	0.23*
1985	0.36
1986	0.47
1987	0.28
1988	0.22*
1989	0.36

Table 7. Summary of parameters used in stock synthesis model. * indicates values that were fixed during a run. ** indicates value determined by constraint, *** indicates values set after run based on other estimated parameters (see text). Fixed and estimated parameters in this table are for synthesis run with initial numbers at age fixed at 22.5 million or 30 million and M (NATMORT) fixed at 0.2.

Parameter	Value (22.5)	Value (30)
NATMORT	0.200 *	.200 *
Trawl selectivity parameters		
TRL INIT	0.001 *	.001 *
TRL 50% YNG		
1980	39.019	39.312
1981	38.479	38.197
1982	39.911	39.103
1983	44.894	44.299
1984	38.156	40.345
1985	42.999	42.505
1986	35.197	34.908
1987	36.811	36.539
1988	40.563	40.196
1989	38.115	37.866
1990	37.949	37.618
1991	40.825	40.544
TRL SLP YNG	0.410	.419
TRL-F 50% OLD	57.953	57.340
TRL-F SLP OLD	0.272	.272
TRL-F FINAL	0.172	.163
TRL-M 50% OLD	52.479	52.229
TRL-M SLP OLD	0.279	.278
TRL-M FINAL	0.225	.213
Set net selectivity parameters		
SET INIT	0.001 *	.001 *
SET 50% YNG	45.918	45.669
SET SLP YNG	0.481	.484
SET-F 50% OLD	61.888	61.545
SET-F SLP OLD	0.620	.610
SET-F FINAL	0.051	.050
SET-M 50% OLD	54.262	54.295
SET-M SLP OLD	0.442	.488
SET-M FINAL	0.056	.054

Table 7 (cont.)

Recreational selectivity parameters

REC INIT	0.020	.022
REC 50% YNG	52.954	52.115
REC SLP YNG	0.116	.114
REC-F 50% OLD	50.428	50.299
REC-F SLP OLD	0.320	.330
REC-F FINAL	0.020	.020
REC-M 50% OLD	41.815	41.625
REC-M SLP OLD	1.028	1.183
REC-M FINAL	0.062	.057

Hook and line/longline selectivity parameters

HOOK INIT	0.001 *	.001 *
HOOK 50% YNG	50.698	49.771
HOOK SLP YNG	0.190	.187
HOOK-F 50% OLD	62.097	61.835
HOOK-F SLP OLD	0.703	.683
HOOK-F FINAL	0.022	.023
HOOK-M 50% OLD	54.531	54.362
HOOK-M SLP OLD	0.782	.754
HOOK-M FINAL	0.100	.100

Triennial survey selectivity parameters

TRI INIT	0.990	.990
TRI 50% YNG	75.000	75.000
TRI SLP YNG	0.574	.574
TRI-F 50% OLD	50.004	49.994
TRI-F SLP OLD	0.041	.037
TRI-F FINAL	0.990 *	.990 *
TRI-M 50% OLD	49.989	49.999
TRI-M SLP OLD	0.166	.183
TRI-M FINAL	0.990	.990

Ageing error parameters

p AGREE. #1	0.750 *	.750 *
p AGREE #21	0.100 *	.100 *

Catchability used with recreational effort

Q-REC FISH	0.063 **	.055 **
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Growth parameters

FEMALE L1	25.000	25.016
FEMALE LINF	75.164	75.175
FEMALE K	0.189	.189
FEMALE CV1	0.087 *	.087 *
MALE CV21	0.045 *	.045 *
MALE L1	27.408	27.435
MALE LINF	64.300	64.367
MALE K	0.234	.233
MALE CV1	0.063	.063
MALE CV21	0.063	.063

Table 7 (cont.)

Additional parameters used to determine virgin biomass			
VIR. RECR. MULT.	0.900 ***	1.009 ***	
REC. STD.	0.500 ***	.500 ***	
Initial numbers at age and recruitment estimates			
INIT AGE 15+	0.550	.603	
INIT AGE 14	0.056	.076	
INIT AGE 13	0.0001	.002	
INIT AGE 12	0.193	.221	
INIT AGE 11	0.054	.050	
INIT AGE 10	0.194	.223	
INIT AGE 9	0.242	.260	
INIT AGE 8	0.104	.129	
INIT AGE 7	0.277	.321	
INIT AGE 6	0.316	.331	
INIT AGE 5	0.264	.334	
INIT AGE 4	1.090	1.004	
INIT AGE 3	2.250 *	3.000 *	
INIT AGE 2	0.600	.604	
RECRUIT 80	1.030	1.096	
RECRUIT 81	0.348	.356	
RECRUIT 82	0.100	.128	
RECRUIT 83	0.025	.028	
RECRUIT 84	1.026	1.112	
RECRUIT 85	1.074	1.195	
RECRUIT 86	0.298	.333	
RECRUIT 87	0.217	.250	
RECRUIT 88	0.891	.993	
RECRUIT 89	1.076	1.241	
RECRUIT 90	0.001	.001	
RECRUIT 91	0.550 ***	.612 ***	

Table 8. Value of likelihood components for synthesis fit when initial numbers at age-3 fixed to 15 million [L(1.5)] through 60 million [L(6.0)] with M=0.2.

LIKELIHOOD TYPE	EMPHASIS	L(1.5)	L(2.25)	L(3.0)	L(6.0)
TRL AGE COMPS	1.0	-142.72	-112.86	-99.21	-100.179
TRL SIZE COMPS	1.000	-274.66	-271.54	-272.29	-275.434
TRL SIZE@AGE	1.0	-229.56	-234.25	-245.58	-247.487
SN SIZE COMPS	1.0	-171.86	-171.02	-171.72	-174.893
REC SIZE COMPS	1.0	-171.15	-172.43	-177.27	-186.436
BKLI SIZE COMPS	1.0	-233.37	-233.36	-229.79	-228.537
TRI SURVEY BIO	1.0	2.65	2.26	1.66	-.434
TRI SIZE COMPS	0.250	-250.51	-241.16	-235.47	-252.341
REC. EFFORT EST	1.0	8.55	8.73	8.86	8.485
PENALTY FUNCTION	10.0	-4.35	-4.07	-3.91	-3.456
TOTAL LIKELIHOOD:		1318.2	-1285.5	-1283.3	-1302.6

Table 9. Estimated (by synthesis) and observed mean lengths (or ages) and fraction of composition female for length and age composition samples. Shown are results for run with initial numbers at age-3 set to 22.5 million and M=0.2.

YR	TYPE	F (or comb.)		M		FRAC F	
		EST	OBS	EST	OBS	EST	OBS
80	TRAWL AGE	5.5	5.6	5.5	5.0	.494	.513
80	TRAWL L	48.9	49.6	47.3	47.0	.494	.515
81	TRAWL AGE	5.8	5.4	6.0	5.6	.497	.524
81	TRAWL L	50.3	48.8	48.6	47.5	.497	.517
82	TRAWL AGE	6.3	6.8	6.6	6.5	.495	.489
82	TRAWL L	52.6	54.1	50.4	50.8	.495	.482
83	TRAWL AGE	7.4	7.6	7.8	6.9	.498	.554
83	TRAWL L	56.1	58.2	53.4	53.5	.498	.570
84	TRAWL AGE	7.7	9.4	8.0	9.0	.476	.444
84	TRAWL L	56.1	60.7	53.2	55.4	.476	.453
85	TRAWL L	58.8	59.3	54.9	55.2	.462	.416
86	TRAWL L	46.7	45.2	45.5	43.0	.458	.478
87	TRAWL L	47.6	46.4	46.9	45.0	.479	.518
88	TRAWL L	51.0	50.3	49.8	48.6	.491	.477
89	TRAWL L	50.3	50.9	48.2	48.2	.475	.392
90	TRAWL L	47.4	47.9	46.0	46.8	.473	.436
91	TRAWL L	48.8	48.7	47.9	47.5	.493	.452
86	SET L	57.9	60.0	53.8	55.8	.514	.452
87	SET L	53.9	53.6	51.5	52.2	.509	.472
88	SET L	52.6	54.3	51.0	50.0	.524	.632
89	SET L	54.0	53.8	51.7	51.1	.532	.542
90	SET L	54.4	53.2	51.5	50.5	.528	.551
91	SET L	52.6	51.8	50.3	50.3	.530	.587
80	REC L	43.6	44.2	(sexes combined)			
81	REC L	45.9	45.0	"			
82	REC L	48.1	48.4	"			
83	REC L	50.6	51.2	"			
84	REC L	47.5	47.3	"			
85	REC L	41.6	38.3	"			
86	REC L	41.7	40.0	"			
87	REC L	43.9	46.0	"			
88	REC L	43.4	43.7	"			
89	REC L	40.5	43.0	"			
86	HOOK L	55.0	55.6	51.1	51.4	.518	.472
87	HOOK L	52.3	50.0	50.2	48.2	.503	.457
88	HOOK L	52.1	54.3	50.3	50.0	.507	.632
89	HOOK L	52.7	53.1	50.1	49.9	.514	.501
90	HOOK L	50.6	45.8	(sexes combined)			
91	HOOK L	51.4	56.8	49.1	52.3	.521	.511
80	TRI L	46.5	43.8	45.1	43.4	.497	.474
83	TRI L	57.4	56.9	53.4	54.0	.479	.465
86	TRI L	46.1	62.0	45.1	50.1	.489	.552
89	TRI L	39.5	32.8	39.9	31.2	.492	.431

Table 11. Length-specific selectivity (x 100) as estimated by synthesis model when initial numbers at age-3 set to 30 million and M=0.2.

Gear	Sex	Total length at bottom of length bin																									
		20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	60	64	68	72	76	80	
setnet	F	0	0	0	0	0	0	0	0	0	0	1	2	6	14	31	55	77	91	97	100	98	75	22	6	5	5
	M	0	0	0	0	0	0	0	0	0	0	1	2	6	14	31	54	74	82	75	56	34	11	6	5	5	5
rec	F	7	10	13	16	20	26	32	40	49	60	71	83	93	100	98	87	69	50	34	15	9	7	7	7	7	7
	M	7	10	13	16	21	28	34	40	49	60	65	77	89	98	101	97	80	61	42	26	15	9	7	7	7	7
hkl1	F	0	0	0	1	1	2	3	4	6	9	13	18	25	33	43	55	68	80	91	100	91	25	4	3	3	3
	M	0	0	0	1	1	2	4	6	9	13	18	25	33	43	55	65	70	56	30	13	12	12	13	13	13	
year:	80																										
trawl	F	0	0	0	0	0	1	2	4	10	21	39	62	81	93	99	100	97	91	82	71	47	30	22	19	18	17
	M	0	0	0	0	0	1	2	4	10	21	39	60	78	88	90	86	78	67	55	45	32	26	24	23	23	
year:	81																										
trawl	F	0	0	0	0	0	1	3	7	15	30	51	72	88	96	100	99	96	90	81	70	46	30	22	19	17	17
	M	0	0	0	0	0	1	3	7	15	30	50	71	85	91	86	77	66	55	44	31	26	23	23	23	22	
year:	82																										
trawl	F	0	0	0	0	0	1	2	5	11	23	42	64	83	94	99	100	97	91	82	71	47	30	22	19	18	17
	M	0	0	0	0	0	1	2	5	11	23	41	63	80	89	91	86	78	67	55	45	32	26	24	23	23	
year:	83																										
trawl	F	0	0	0	0	0	0	0	1	3	8	17	33	55	78	93	100	98	90	79	52	33	24	21	20	19	18
	M	0	0	0	0	0	0	0	1	3	8	16	32	52	71	81	80	72	61	50	35	29	27	26	25	25	
year:	84																										
trawl	F	0	0	0	0	0	1	3	7	15	30	51	72	89	97	100	98	92	83	72	48	30	22	19	18	18	18
	M	0	0	0	0	0	1	3	7	15	29	50	70	84	89	86	78	68	56	46	32	26	24	23	23	23	
year:	85																										
trawl	F	0	0	0	0	0	0	1	3	7	15	29	51	73	90	98	100	95	87	75	50	32	20	19	18	18	
	M	0	0	0	0	0	0	1	3	7	15	29	49	70	83	85	80	70	58	48	34	28	25	25	24	24	
year:	86																										
trawl	F	0	0	0	2	5	11	23	42	63	81	92	98	100	99	97	93	87	79	68	45	29	21	18	17	17	
	M	0	0	0	2	5	11	23	42	63	80	91	95	94	91	84	75	64	53	43	30	25	23	22	22	22	
year:	87																										
trawl	F	0	0	0	1	2	6	13	27	46	68	85	94	99	100	98	94	88	80	69	46	29	21	18	17	17	
	M	0	0	0	1	2	6	13	27	46	67	83	91	93	91	85	76	65	54	44	31	25	23	22	22	22	
year:	88																										
trawl	F	0	0	0	0	0	1	3	7	16	31	52	74	89	97	100	97	92	83	72	48	30	22	19	18	18	
	M	0	0	0	0	0	1	3	7	16	31	51	72	85	89	86	78	67	56	46	32	26	24	23	23	23	
year:	89																										
trawl	F	0	0	0	0	1	3	8	17	33	54	75	89	97	100	99	95	89	81	70	46	29	22	18	17	17	
	M	0	0	0	0	1	3	8	17	33	54	74	87	92	91	86	77	66	54	44	31	25	23	23	22	22	
year:	90																										
trawl	F	0	0	0	0	1	4	9	19	35	57	77	91	97	100	99	95	89	81	70	46	29	21	18	17	17	
	M	0	0	0	0	1	4	9	19	35	56	76	88	92	91	85	77	66	54	44	31	25	23	23	22	22	
year:	91																										
trawl	F	0	0	0	0	1	3	6	14	28	48	71	88	97	100	98	92	84	72	48	31	22	19	18	18	18	
	M	0	0	0	0	1	3	6	14	28	48	69	83	89	86	79	68	56	46	32	26	24	24	23	23	23	
year:	92																										

Table 12. Numbers at age (0000), by sex, as estimated by the synthesis model when total initial numbers at age-3 were fixed at 22.5 million and M=2.

Females																					
Yr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
80	515	300	1125	544	131	157	138	51	121	97	27	96	0	28	274	0	0	0	0	0	0
81	173	416	234	797	360	87	109	99	38	91	74	21	75	0	22	216	0	0	0	0	0
82	50	141	329	168	539	243	160	78	73	28	70	57	16	58	0	17	170	0	0	0	0
83	12	40	110	229	106	340	160	42	56	54	21	53	44	12	45	0	13	132	0	0	0
84	513	9	32	83	152	66	216	106	29	40	39	16	40	33	9	34	0	10	102	0	0
85	536	417	7	21	48	89	40	137	71	20	28	29	12	30	25	7	26	0	7	78	0
86	148	435	332	5	14	31	58	27	97	51	15	21	22	9	23	19	3	20	0	6	62
87	108	120	333	227	3	8	17	34	17	65	36	11	16	17	7	18	15	4	16	0	53
88	445	88	94	237	144	2	4	10	22	11	47	27	18	12	13	5	14	12	3	12	42
89	538	363	70	69	155	89	1	3	7	15	8	35	20	16	9	10	4	11	9	2	43
90	0	437	284	49	43	91	52	0	1	4	11	6	26	15	4	7	7	3	8	7	35
91	-	0	342	196	29	24	51	31	0	1	3	8	4	19	11	3	5	6	2	6	33

Males																					
Yr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
80	515	300	1125	544	131	157	138	51	121	97	27	96	0	28	274	0	0	0	0	0	0
81	173	414	231	810	391	95	116	103	39	91	73	20	73	0	21	211	0	0	0	0	0
82	50	141	324	167	570	277	169	85	77	29	69	56	15	56	0	16	162	0	0	0	0
83	12	40	108	229	115	398	197	50	62	57	21	52	42	11	42	0	12	122	0	0	0
84	513	9	32	82	163	79	273	137	35	45	41	16	38	31	6	31	0	9	91	0	0
85	536	416	7	20	50	101	51	182	94	24	31	29	11	27	22	16	22	0	6	66	0
86	148	434	329	5	15	35	72	36	133	70	18	24	22	8	21	17	4	17	0	5	51
87	108	119	326	228	3	9	23	48	25	94	50	13	17	16	6	13	12	3	13	0	42
88	445	88	92	232	152	2	6	15	33	18	68	37	10	13	12	4	11	9	7	9	32
89	538	362	70	68	159	101	1	4	11	24	13	50	27	17	9	9	3	8	7	2	32
90	0	435	280	49	45	102	66	1	3	7	17	9	37	20	5	7	6	2	6	5	25
91	-	0	336	193	31	28	64	43	0	2	5	12	7	27	14	4	5	5	2	4	23

Table 13. Numbers at age (0000), by sex, as estimated by the synthesis model when total initial numbers at age-3 were fixed at 30 million and M=0.2.

Females

Yr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
80	547	302	1500	501	166	165	160	64	129	111	24	110	0	38	301	0	0	0	0	0	0
81	177	443	236	1079	338	113	116	117	88	99	86	19	86	0	30	238	0	0	0	0	0
82	64	144	352	173	748	236	81	83	68	37	77	67	15	68	0	23	189	0	0	0	0
83	14	51	112	247	112	491	162	58	63	66	28	59	52	11	53	0	18	149	0	0	0
84	555	11	41	85	168	73	327	111	41	46	50	21	46	40	9	41	0	14	116	0	0
85	597	452	9	29	53	104	47	219	78	39	34	37	16	35	31	7	32	0	11	90	0
86	166	485	361	6	20	36	71	13	160	59	34	26	29	13	27	24	5	25	0	9	72
87	125	134	374	253	4	12	22	46	22	114	43	17	20	23	10	21	19	4	20	0	72
88	496	101	106	271	168	2	7	14	31	116	84	32	13	16	18	17	15	3	16	51	41
89	620	404	81	79	184	109	1	5	10	22	12	64	23	10	12	14	6	13	12	2	51
90	0	504	319	58	51	116	69	1	3	7	17	9	49	19	8	9	11	4	10	9	48
91	306	0	397	226	37	32	72	44	0	2	5	12	7	38	15	6	7	8	3	6	42

Males

Yr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
80	547	302	1500	501	166	165	160	64	129	111	24	110	0	38	301	0	0	0	0	0	0
81	177	441	234	1096	366	123	123	121	49	99	83	19	83	0	29	233	0	0	0	0	0
82	64	144	347	171	787	265	90	92	91	37	76	66	10	66	0	22	181	0	0	0	0
83	14	51	111	247	121	564	193	67	69	69	28	58	50	11	50	0	17	139	0	0	0
84	555	11	41	85	179	85	399	139	49	51	51	21	43	18	8	38	0	13	106	0	0
85	597	452	9	29	56	117	57	277	98	35	37	37	15	38	28	6	28	0	10	79	0
86	166	483	358	6	21	40	85	42	207	74	26	28	29	12	28	6	28	0	10	79	0
87	125	134	367	255	4	14	27	60	30	152	55	20	21	22	23	21	4	22	0	7	62
88	492	104	267	176	3	9	19	43	22	113	41	15	16	16	9	19	16	3	17	0	53
89	620	403	81	78	188	121	2	7	14	32	16	86	31	11	16	7	14	12	2	13	41
90	0	502	314	58	53	127	83	1	5	10	23	12	64	24	18	9	11	9	2	42	42
91	306	0	391	223	39	35	85	57	1	3	7	17	9	48	18	6	7	4	8	7	34
																				3	6
																					31

Table 14. Average estimated recruitment for 1980-1990, 1971-1979, and 1971-1990 (10's of millions) for four levels of fixed initial numbers at age 3, I3, in tens of millions. Recruitment estimates prior to 1980 are based on an assumed total mortality rate (Z) of 0.25.

Period	Initial numbers at age-3			
	1.5	2.25	3.0	6.0
71-79 (early)	1.42	1.56	1.79	4.65
80-90 (recent)	0.52	0.55	0.61	1.43
71-90 (total)	0.92	1.01	1.14	2.88
early/recent	2.77	2.83	2.93	3.25

Table 15. Estimate biomass (MT) and spawning stock (billions of eggs) in 1980 and in 1991 for four levels of initial numbers at age 3, I3 (10's of millions).

	Initial numbers at age-3			
	1.5	2.25	3.0	6.0
1980				
Biomass	57241	63678	72194	211468
Spawning Stock	9992	11107	12450	41334
1991				
Biomass	12844	16623	21890	89312
Spawning Stock	1846	2665	3782	18336

Table 16. Quantities used in equilibrium yield calculations. s_{xxy} , and w_{xy} are selectivity and mean weight (kg) at age for gear xy (tr, sn, rc, hk) and sex y (f, m). These were taken from the 13=2.25 run (see Table 1 from 1991). TL and W are the population mean total length (cm) and weight (kg) at age. IL was calculated from growth parameters estimated by the 13=2.25 run. W is calculated based on the length weight relationship in Table 7, part a, the proportion of females mature and egg/kg is millions of eggs per kg at age. p_{mat} was calculated as a function of TL and egg/kg as a function of W using equations in Table 7. Yield was calculated assuming that F (at selectivity = 1.0) for hk , sn and rc relative to $trawl$ were 0.705, 0.724 and 0.326.

Age	snrf	wrf	strm	wtrm	semf	wmf	ssmf	wnmf	arcf	wrcf	stcm	wrcm	shkf	whkf	shkm	whkm
1	0	0.14	0	0.17	0	0.12	0	0.16	0.12	0.12	0.17	0.16	0	0.14	0.14	0.17
2	0	0.38	0.09	0.4	0	0.38	0	0.41	0.35	0.32	0.4	0.36	0	0.05	0.01	0.37
3	0.46	0.62	0.48	0.62	0.1	0.7	0.1	0.68	0.69	0.58	0.49	0.54	0.18	0.18	0.61	0.66
4	0.87	0.87	0.78	0.82	0.5	0.94	0.42	0.89	0.9	0.85	0.19	0.69	0.43	0.43	0.91	0.86
5	0.92	1.14	0.78	1.01	0.85	1.2	0.65	1.26	0.97	1.09	0.1	1.01	0.7	1.22	0.39	0.82
6	0.8	1.42	0.68	1.2	0.94	1.46	0.63	1.32	0.5	1.34	0.1	1.29	0.87	1.5	0.54	1.06
7	0.65	1.67	0.58	1.37	0.85	1.69	0.52	1.33	0.31	1.59	0.11	1.48	0.88	1.72	0.47	1.06
8	0.41	1.9	0.5	1.51	0.68	1.87	0.42	1.43	0.21	1.59	0.12	1.65	0.75	1.89	0.38	1.44
9	0.41	2.13	0.45	1.64	0.49	2.02	0.37	1.53	0.11	2.07	0.13	1.78	0.56	2.02	0.31	1.45
10	0.34	2.24	0.41	1.74	0.34	2.16	0.27	1.6	0.11	2.07	0.14	1.89	0.38	2.14	0.26	1.65
11	0.3	2.3	0.38	1.83	0.24	2.29	0.23	1.66	0.09	2.1	0.14	1.98	0.26	2.24	0.23	1.73
12	0.26	2.33	0.36	1.91	0.17	2.45	0.2	1.73	0.08	2.14	0.15	2.06	0.18	2.37	0.21	1.81
13	0.25	2.61	0.35	1.97	0.13	2.59	0.16	1.77	0.08	2.14	0.15	2.12	0.13	2.48	0.2	1.87
14	0.23	2.86	0.35	2.01	0.1	2.73	0.15	1.81	0.07	2.14	0.15	2.21	0.08	2.71	0.18	1.93
15	0.22	3.1	0.33	2.03	0.09	2.86	0.15	1.85	0.07	2.14	0.15	2.24	0.06	2.91	0.17	2.01
16	0.21	3.2	0.32	2.09	0.07	3.04	0.14	1.87	0.07	2.14	0.15	2.26	0.05	3.07	0.16	2.08
17	0.21	3.27	0.32	2.12	0.07	3.12	0.13	1.91	0.07	2.14	0.15	2.28	0.05	3.14	0.16	2.09
18	0.21	3.3	0.32	2.14	0.06	3.2	0.13	1.94	0.07	2.14	0.15	2.3	0.04	3.19	0.16	2.11
19	0.2	3.33	0.32	2.15	0.06	3.26	0.13	1.96	0.07	2.14	0.16	2.31	0.04	3.19	0.16	2.11
20	0.2	3.46	0.31	2.17	0.06	3.31	0.13	1.96	0.07	2.14	0.16	2.33	0.04	3.31	0.16	2.14
21	0.2	3.51	0.31	2.19	0.06	3.42	0.12	1.98	0.07	2.14	0.16	2.33	0.04	3.31	0.16	2.14
Age	TL	W	pmat	egg/kg (mill.)												
1	25	0.12	0.001	0.225011												
2	33.64	0.31	0.017	0.240353												
3	40.79	0.56	0.122	0.261159												
4	46.71	0.84	0.433	0.28527												
5	51.61	1.15	0.758	0.310716												
6	53.67	1.45	0.910	0.33598												
7	59.03	1.74	0.964	0.360023												
8	61.81	2.01	0.983	0.382214												
9	64.11	2.23	0.991	0.402233												
10	66.01	2.46	0.995	0.419981												
11	68.59	2.64	0.997	0.435506												
12	70.87	2.80	0.998	0.448944												
13	73.13	3.06	0.999	0.47031												
14	75.11	3.16	0.999	0.478649												
15	76.89	3.25	0.999	0.485689												
16	78.22	3.32	0.999	0.491612												
17	79.13	3.38	0.999	0.496591												
18	80.13	3.43	0.999	0.500739												
19	81.50	3.47	0.999	0.504213												
20	83.19	3.50	0.999	0.507109												
21	84.02	3.50	0.999	0.507109												

Table 17. Projections of bocaccio biomass and spawning stock (billions of eggs) at the beginning of the year, and F (at selectivity=1.0) for four fisheries, at two fixed levels initial numbers at age 3. The projections assume landings in 1992-1995 are the same as landings in 1991. V1 indicates the equilibrium unfished condition assuming average 1971-1990 recruitment, V2 indicates equilibrium unfished condition assuming average 1980-1990 recruitment.

Initial numbers at Age 3 = 2.25

YEAR	BIOMASS (mt)	EGGS (billions)	F			
			trawl	setnet	rec.	hook&line
V1	54687	10736	0	0	0	0
V2	29986	5887	0	0	0	0
92	15978	2531	.088	.069	.042	.082
93	15430	2429	.097	.071	.045	.081
94	15014	2262	.101	.077	.046	.084
95	14718	2106	.101	.079	.045	.088
96	14523	1999	.100	.079	.044	.088

Initial numbers at Age 3 = 3.0

YEAR	BIOMASS (mt)	EGGS (billions)	F			
			trawl	setnet	rec.	hook&line
V1	72194	12204	0	0	0	0
V2	33265	6538	0	0	0	0
92	21026	3600	.069	.053	.035	.061
93	20271	3464	.076	.054	.038	.060
94	19661	3257	.080	.059	.039	.063
95	19181	3054	.081	.061	.038	.066
96	18828	2904	.080	.061	.038	.067

Table 18. Projections of bocaccio biomass and spawning stock (billions of eggs) at the beginning of the year, and F (at selectivity=1.0) for four fisheries, at two fixed levels of initial numbers at age 3. The projections assume landings in 1992 are the same as landings in 1991, and total landings in 1993-1995 are equal to 1100 mt (the current harvest guideline), allocated to the fisheries in proportion to 1991 landings.

Initial numbers at Age 3 = 2.25

YEAR	BIOMASS (mt)	EGGS (billions)	F			
			trawl	setnet	rec.	hook&line
92	15978	2531	.088	.069	.042	.082
93	15430	2429	.060	.044	.028	.050
94	15644	2376	.060	.045	.027	.049
95	15960	2340	.057	.044	.026	.048
96	16345	2353	.054	.041	.025	.046

Initial numbers at Age 3 = 3.0

YEAR	BIOMASS (mt)	EGGS (billions)	F			
			trawl	setnet	rec.	hook&line
92	21026	3600	.069	.053	.035	.061
93	20271	3464	.048	.034	.024	.038
94	20294	3374	.048	.035	.023	.038
95	20425	3295	.047	.035	.022	.038
96	20647	3270	.046	.034	.022	.037

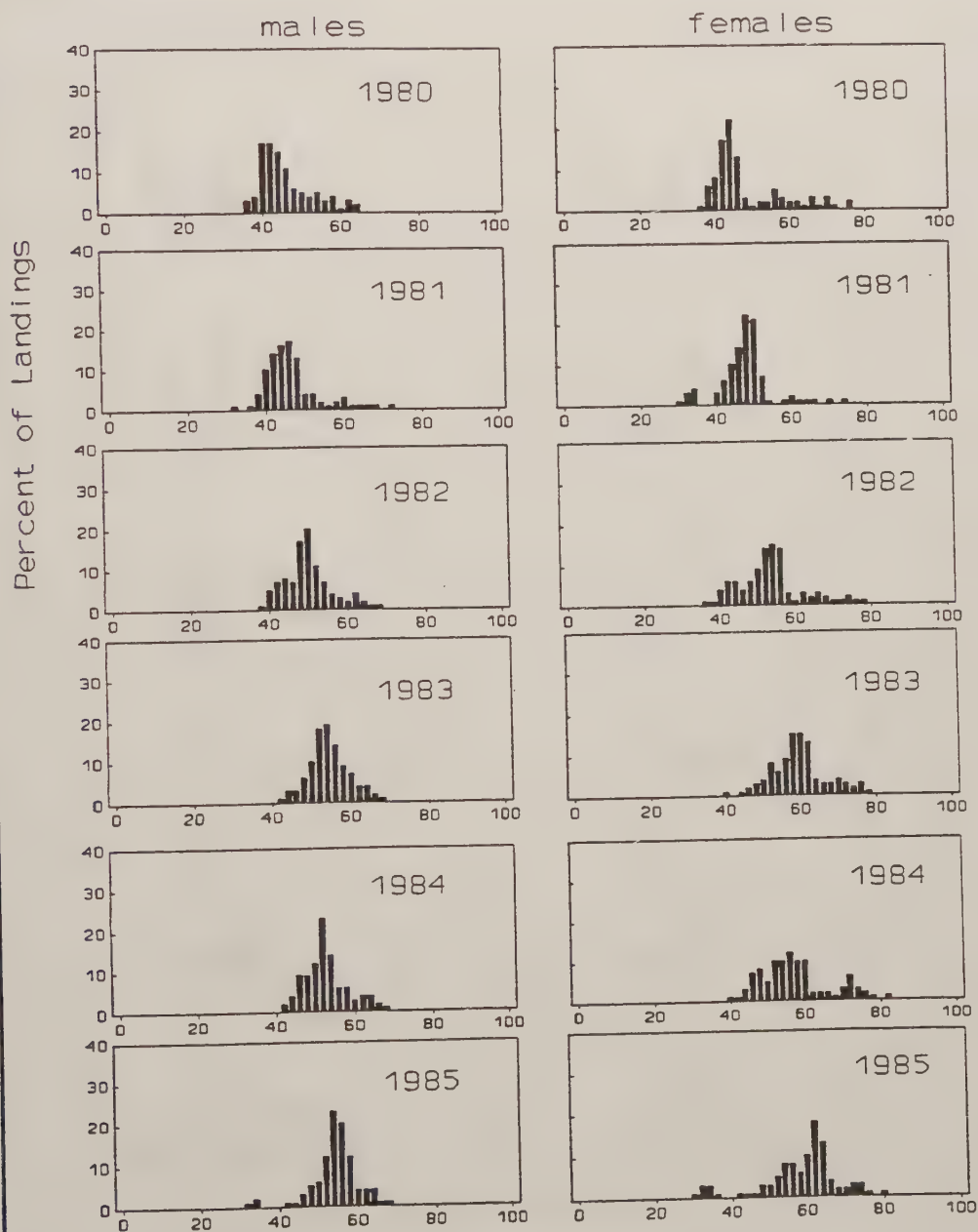


Figure 1 (1/2). Length composition data for bocaccio based on samples from the California trawl fishery landings.

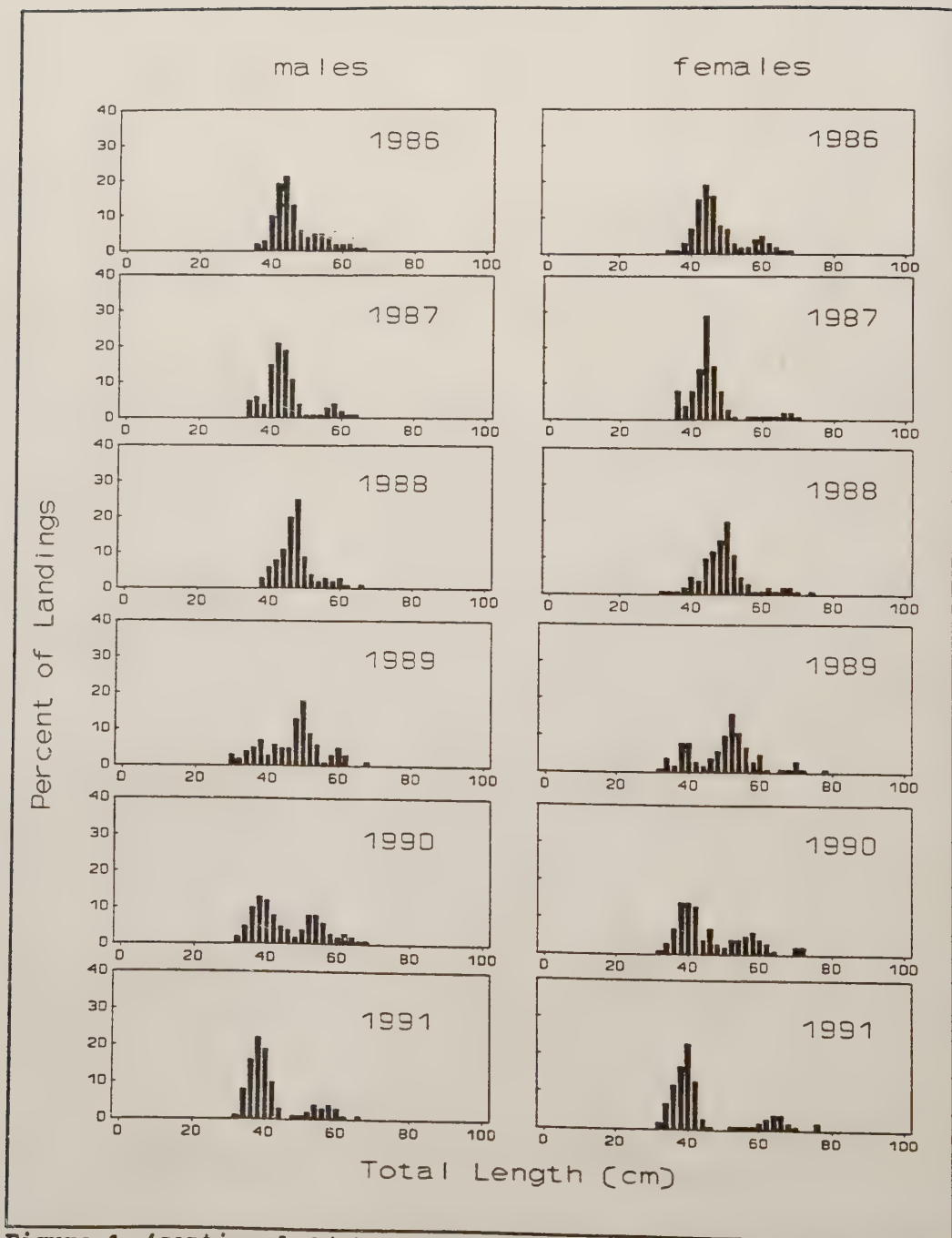


Figure 1 (continued 2/2). Length composition data for bocaccio based on samples from the California trawl fishery landings.

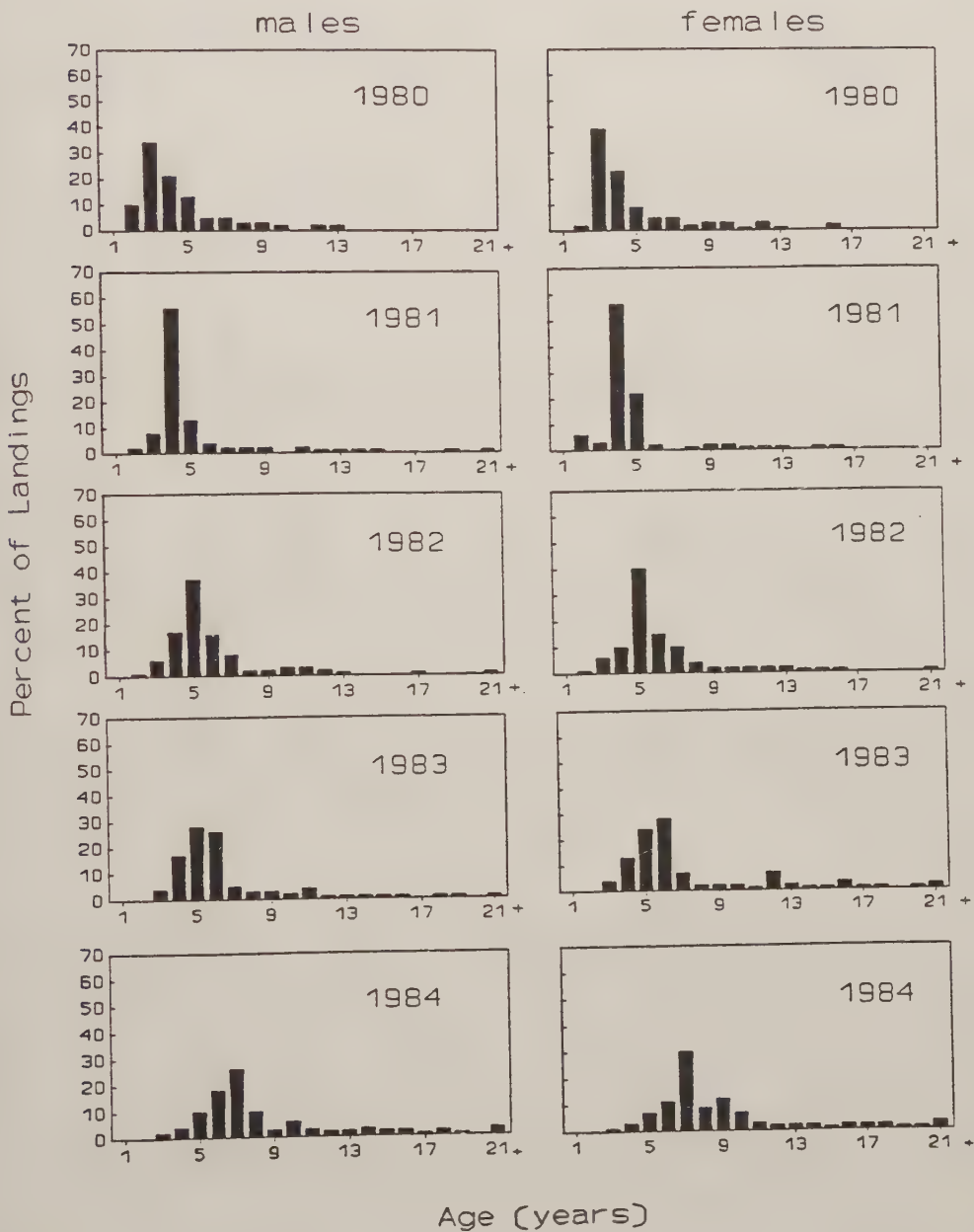


Figure 2. Age composition data for bocaccio based on samples from the California trawl fishery landings.

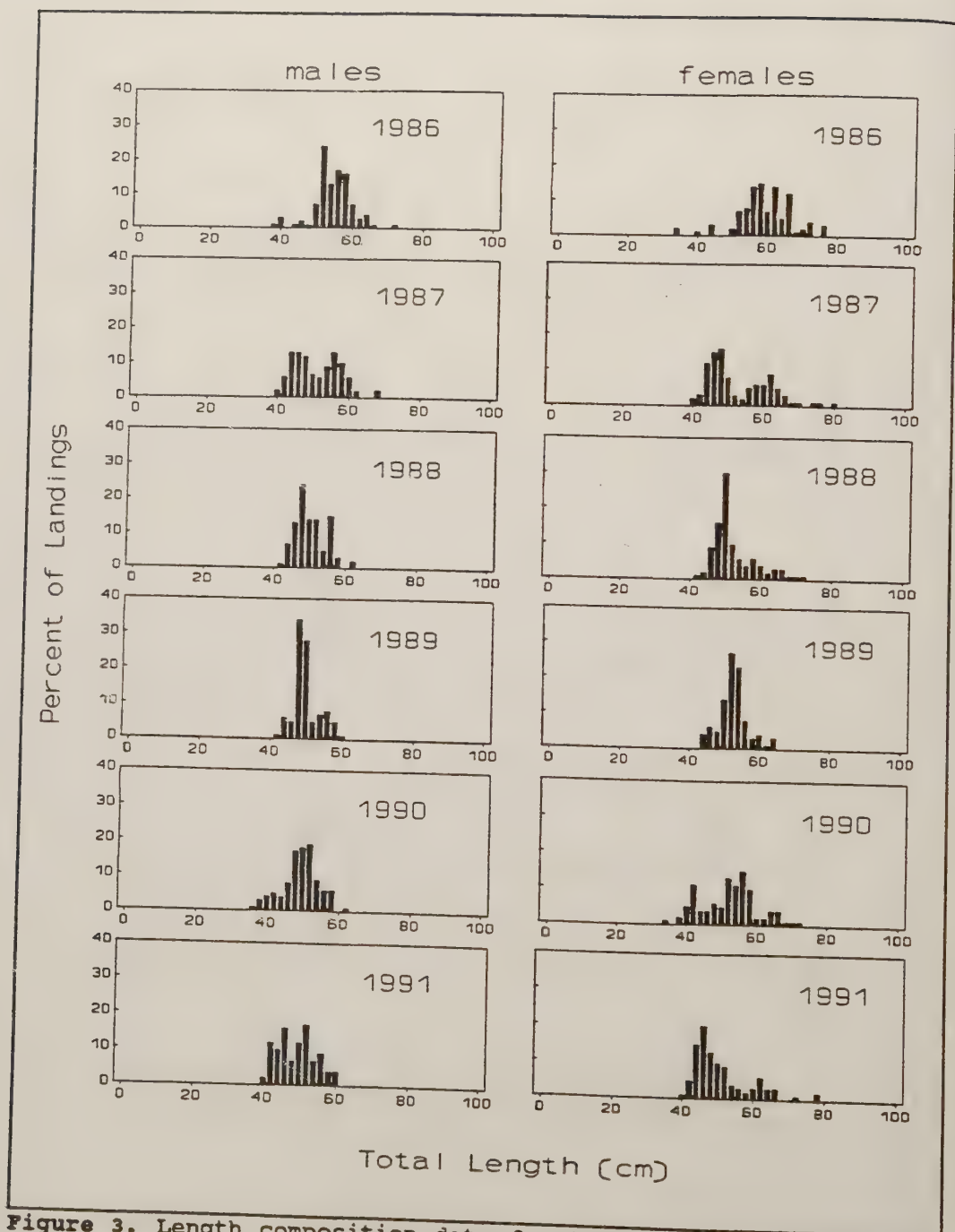


Figure 3. Length composition data for bocaccio based on samples from the California set-net fishery landings.

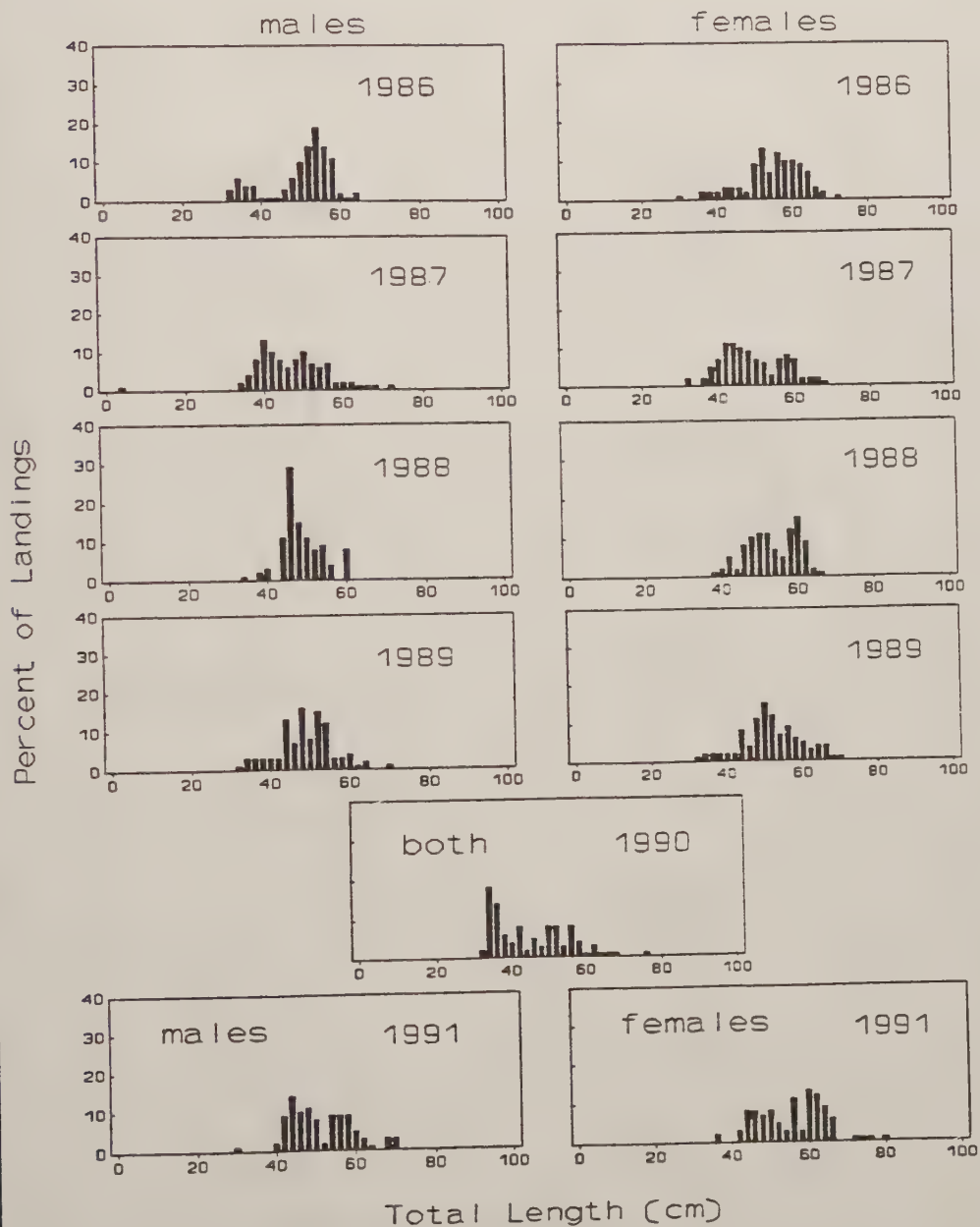


Figure 4. Length composition data for bocaccio based on samples from the California hook-and-line/longline fishery.

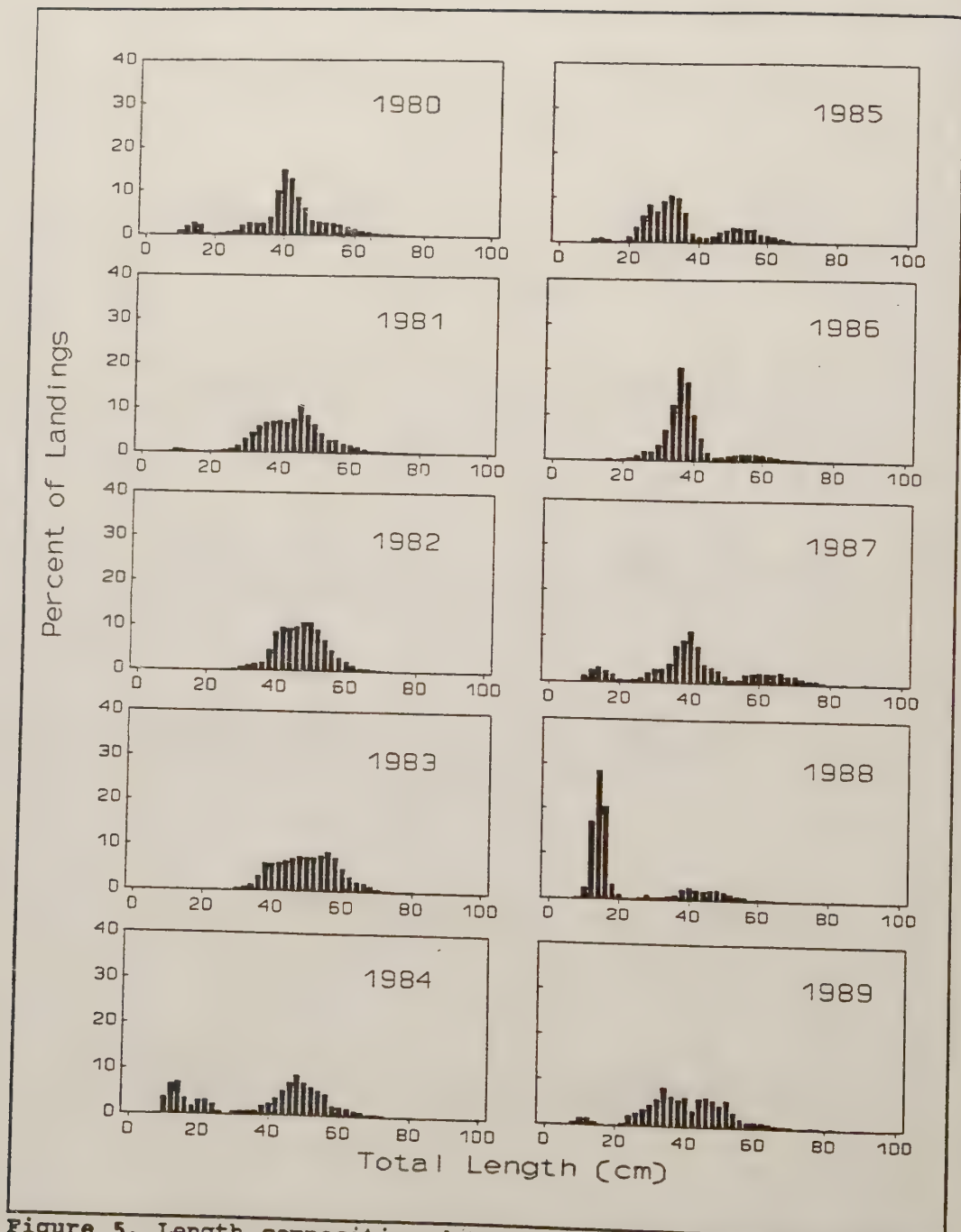


Figure 5. Length composition data for bocaccio based on samples from the California recreational fishery landings.

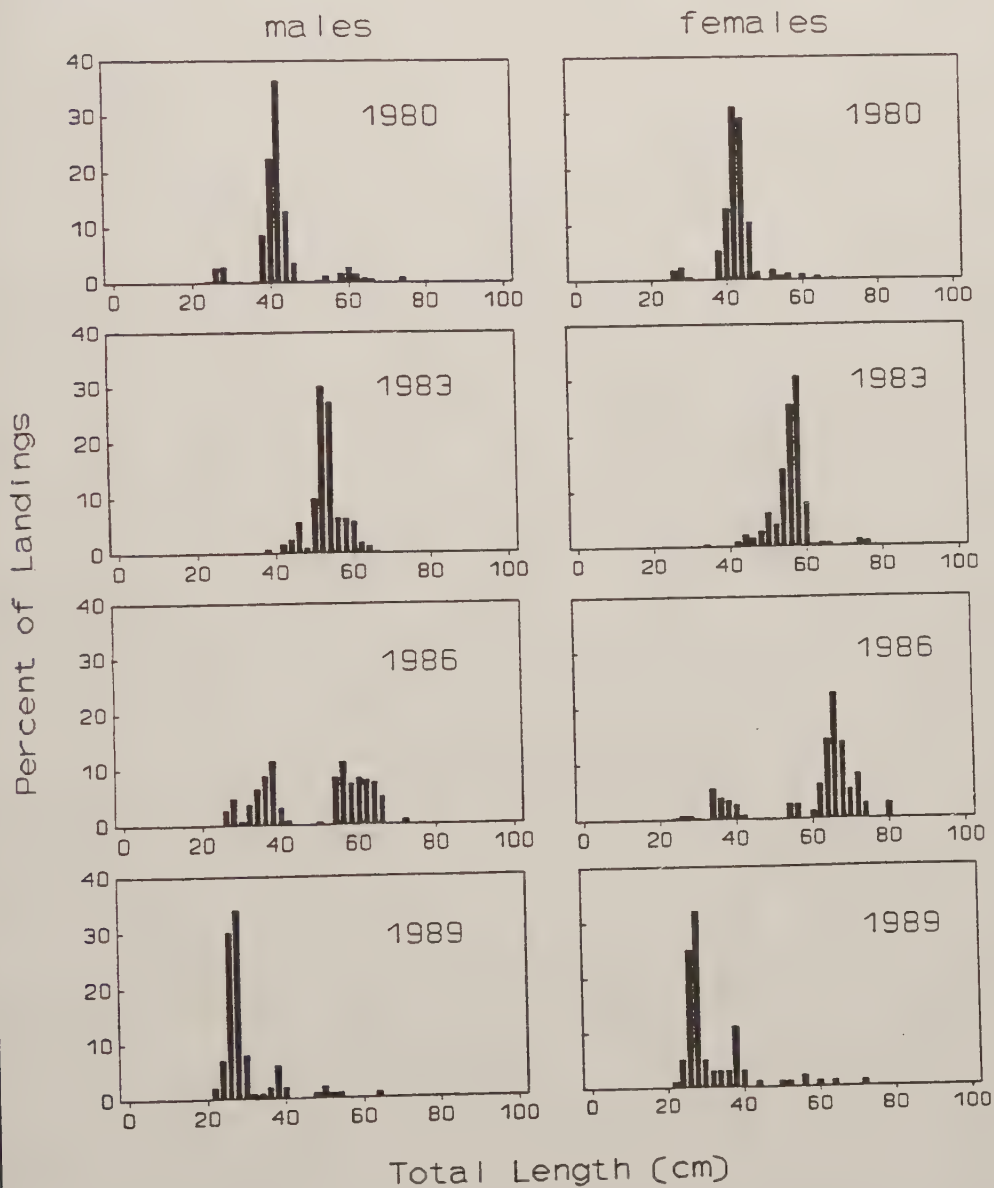


Figure 6. Length composition data for bocaccio based on samples from the NMFS triennial bottom trawl surveys.

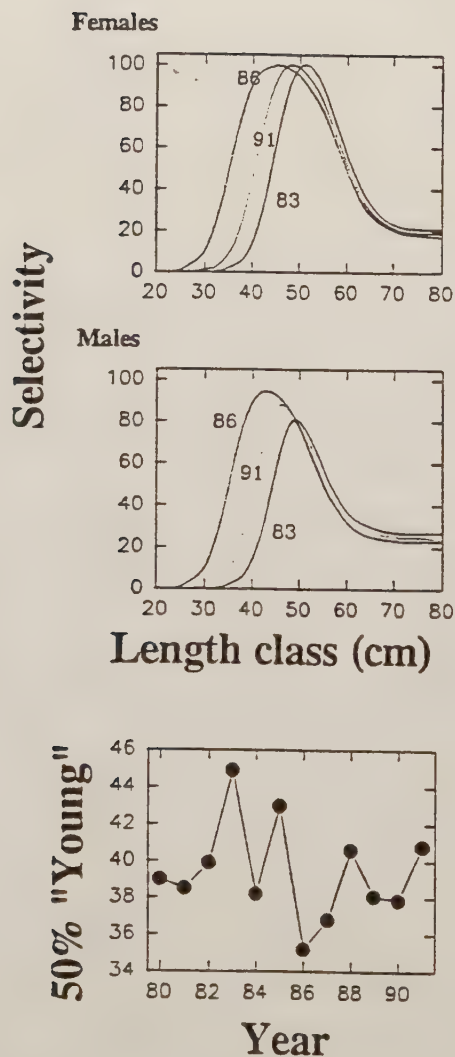


Figure 7. Selectivity of commercial trawl as a function of total length for female and male bocaccio (top and middle panels), and temporal variation in inflection point (cm) of the ascending limb of the selectivity function (50% young), the parameter that introduces time-dependent selectivity.

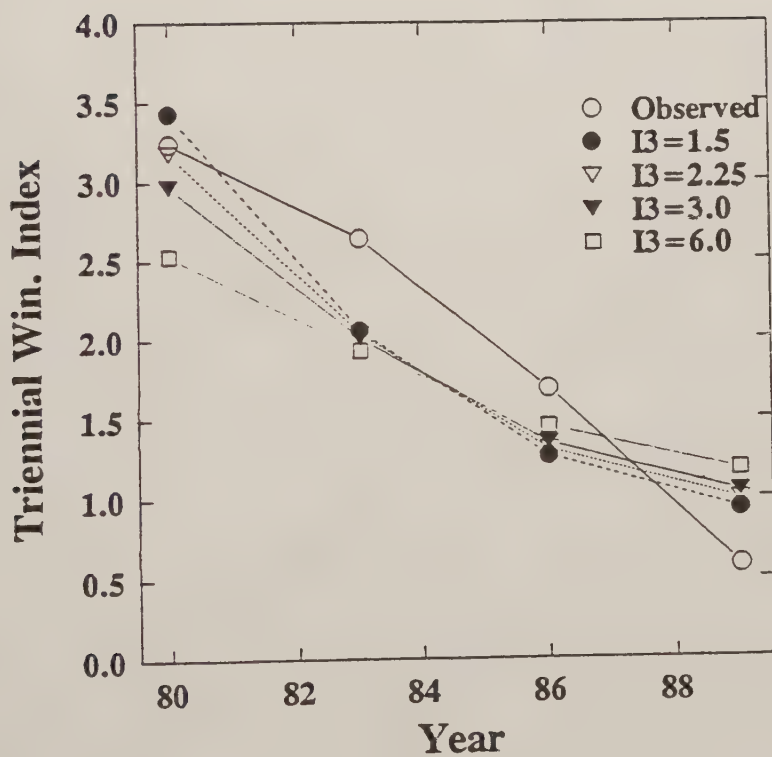


Figure 8. Observed and estimated values (at four fixed levels of initial numbers at age-3 [$I3$]) of the triennial winsorized index over time.

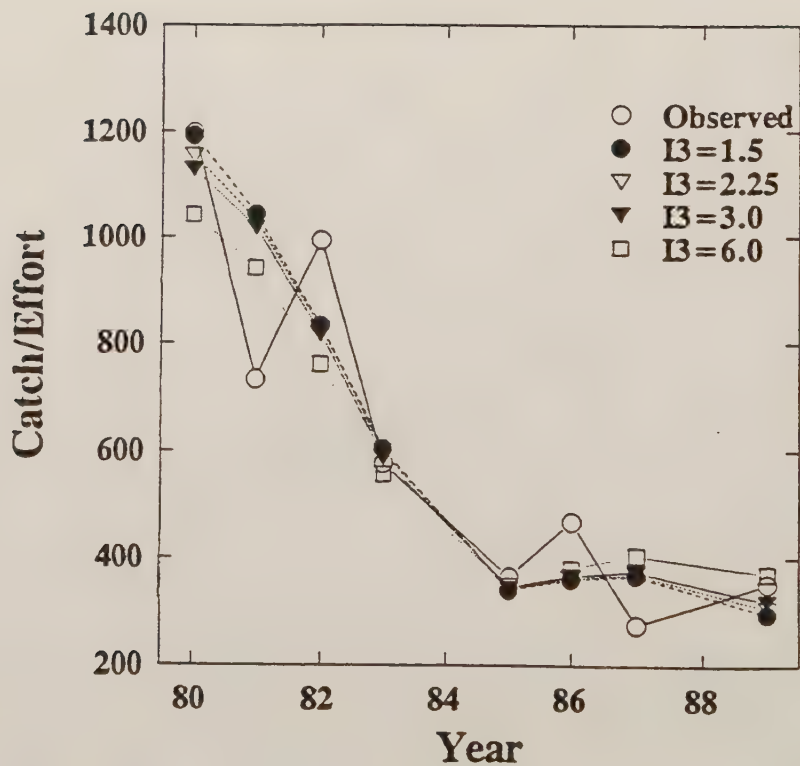


Figure 9. Observed and estimated (at four fixed levels of initial numbers at age-3 [I_3]) of Recreational catch/effort (see text) over time.

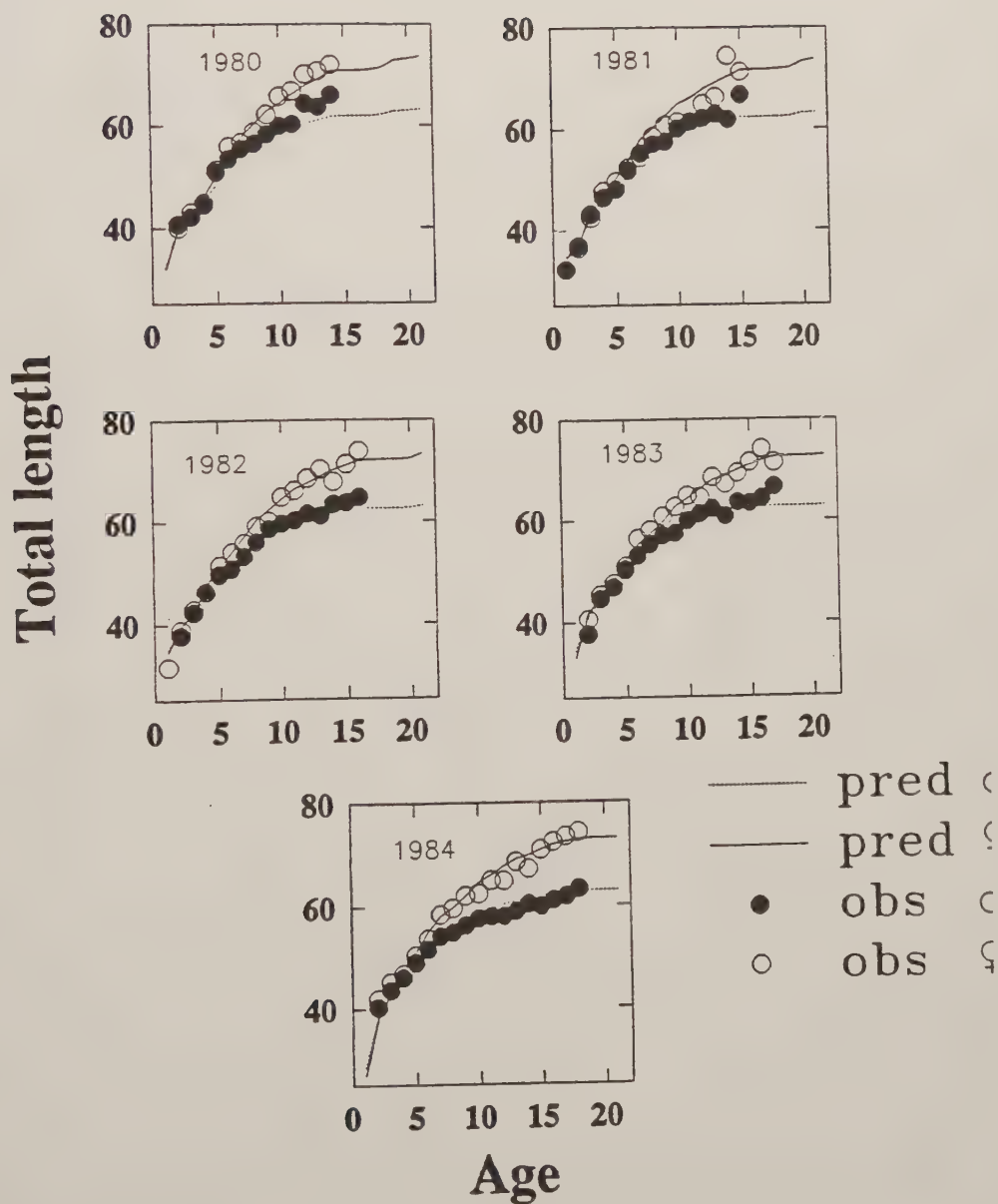


Figure 10. Observed and predicted (at $I3=2.25$) length at age for trawl landings.

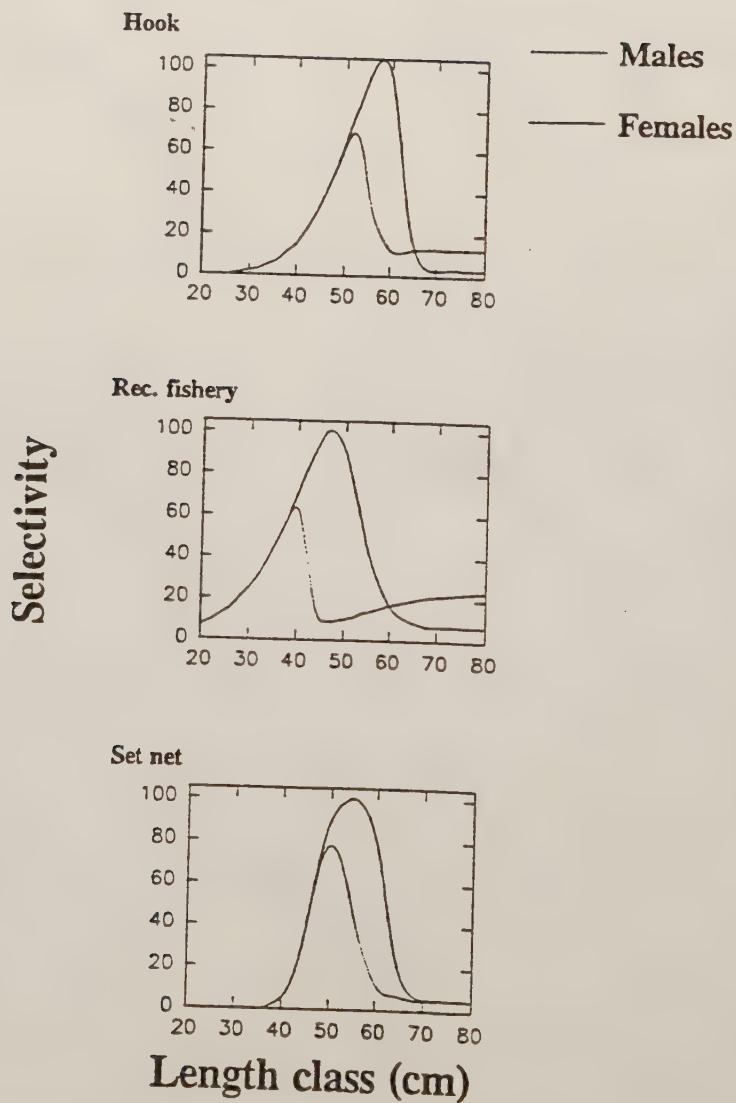


Figure 11. Estimated selectivity versus length (at $I3=2.25$) for hook and line, recreational and set net fisheries.

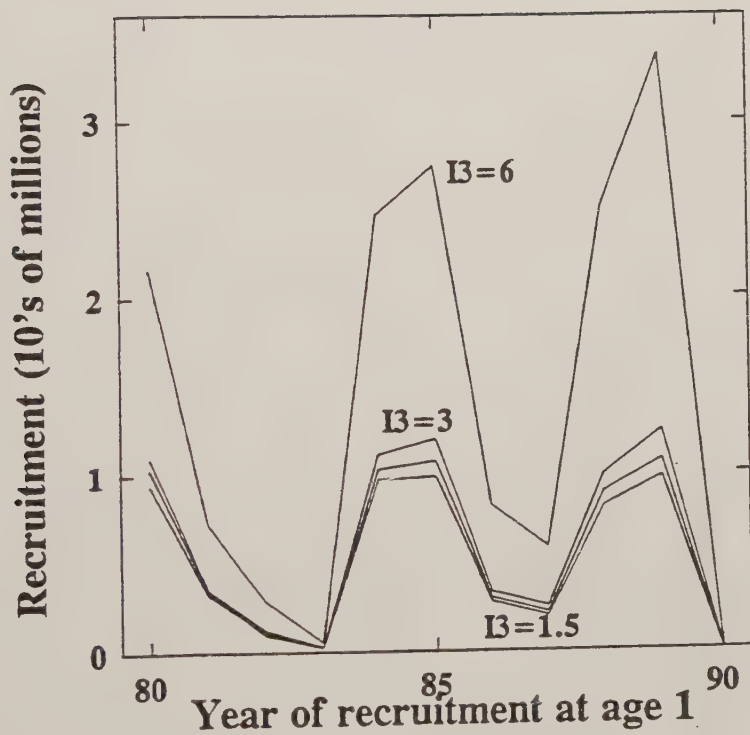


Figure 12. Estimated recruitment over time at four fixed levels of I_3 .

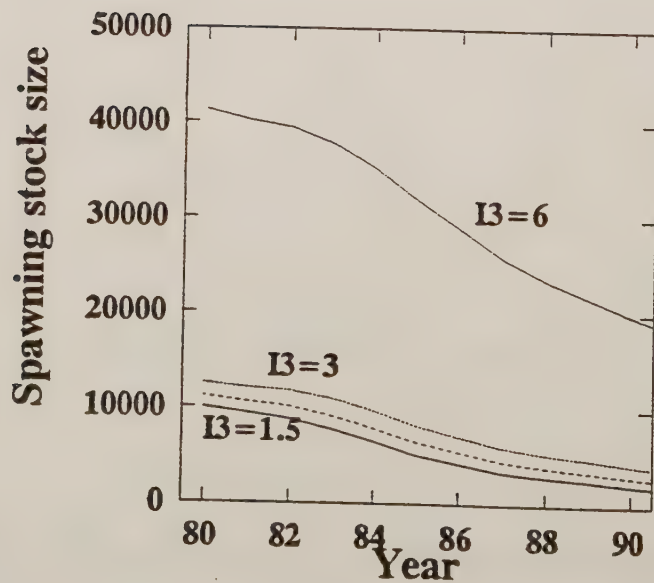
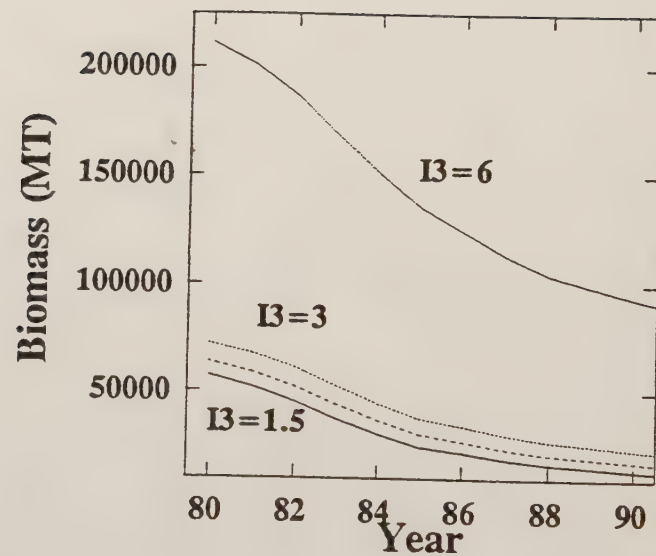


Figure 13. Estimated biomass (top panel) and spawning stock size in billions of eggs (bottom panel) over time for four fixed levels of I_3 .

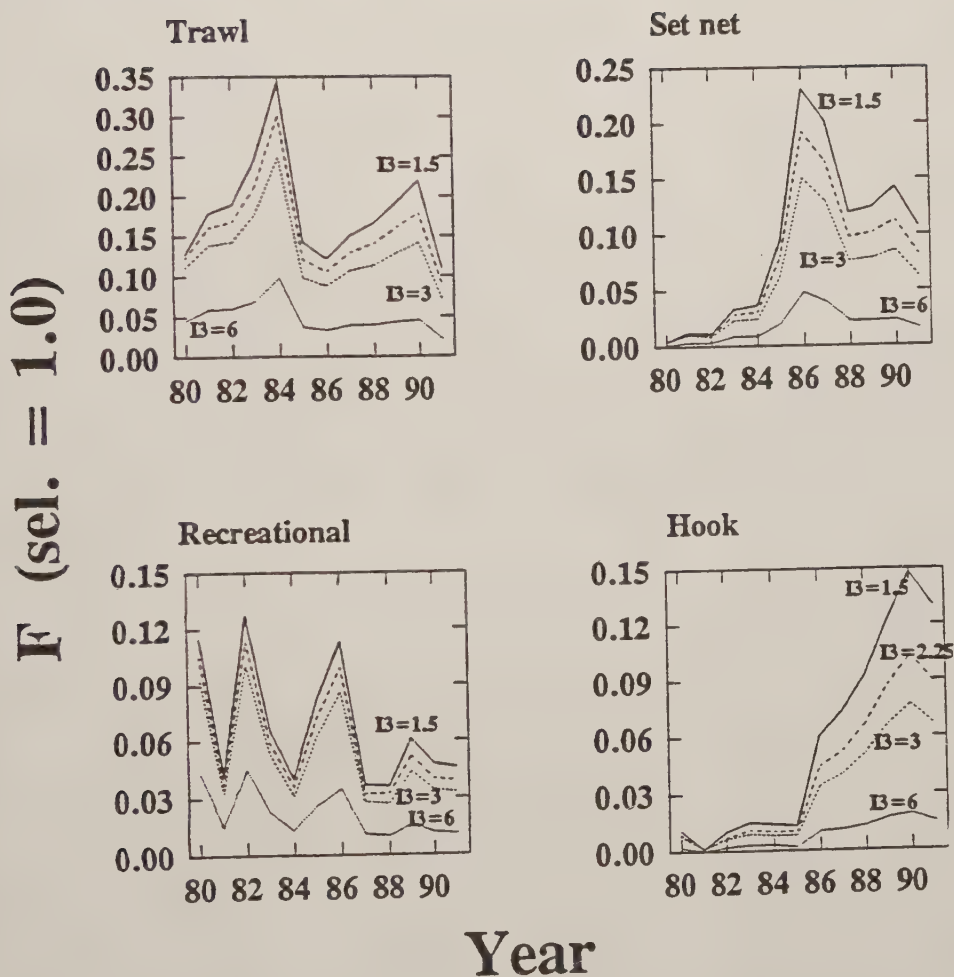


Figure 14. Estimated fishing mortality (for selectivity of 1.0) over time for each of four fisheries. Results are shown for four levels of fixed B .

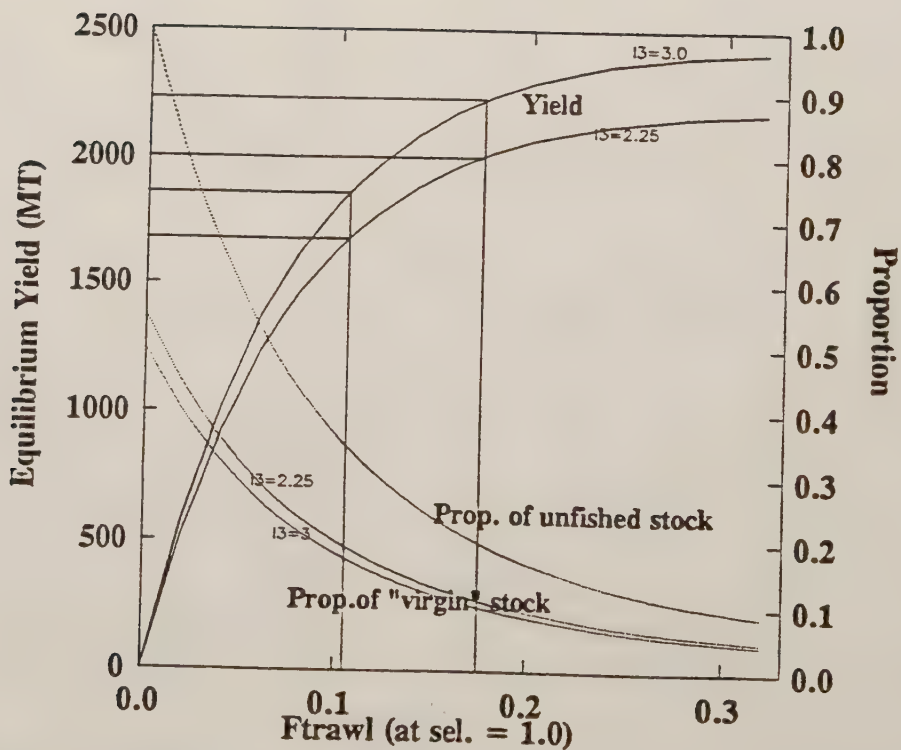


Figure 15. Equilibrium yield results. Increasing functions are yield for the two preferred levels of I_3 versus the F at selectivity = 1.0 for the trawl fishery. Vertical lines intersect these curves at $F=F_{2\%}$ and $F=F_{3\%}$, and the horizontal lines indicate the corresponding yield. The descending functions indicate the equilibrium size of the spawning stock as a proportion of either the unfished stock or the "virgin" stock (see text).

**Attachment 1: Estimation of commercial landings
and the assignment of unknown sex individuals in composition data**

The trawl landing estimates for bocaccio (and chilipepper) were calculated by apportioning rockfish market category landings to the appropriate species, for each port complex/quarter combination based on samples of the landings. This is the standard "CSUM" expansion done as part of the cooperative CDF&G and NMFS groundfish sampling program. These expansions were recalculated in May 1992 using recently updated data sets. Landing figures at this stage differ from previous values because improvements in data processing have made the databases more complete.

These trawl landings estimates were then adjusted in three ways. First, a certain portion of the reported landings in California have no reported gear code. We upwardly adjusted California landings to account for trawl landings with an unreported gear code. To do this, we first calculated the reported landings of mixed rockfish (market categories likely to contain significant numbers of chilipepper or bocaccio) for trawl, hook and line / longline, set net, and other gear (largely unreported gear code) for each INPFC area for each year. We then calculated the proportion known trawl landings made up of the known trawl, hook- and-line / longline, and set-net landings. We then allocated that proportion of the "other" gear landings to trawl.

Our second adjustment was to incorporate landings from southern California. In recent years, landings from south of the Morro Bay port complex have accounted for only a few percent of the trawl landing of mixed rockfish. Consequently almost no trawl sampling has been done south of Morro Bay (Attachment Table 1) and expansions generally have not been performed for southern California. However, in earlier years the southern ports accounted for a larger portion of the Conception area landings, exceeding 10% in several years, and reaching 40% of the Morro Bay landings in one year. To take this into account, we simply multiplied the Conception area landings generated by the expansion by a factor of $(MB+SC)/MB$, where MB and SC are the Morro Bay and Southern California landings of mixed rockfish. Finally, we added in landings from the Oregon portion of the Eureka INPFC area.

For the set-net and hook-and-line fisheries, apportionment to species by port complex and quarter was generally not possible, because in many years few or no samples were collected for a given port complex (Attachment Table 1). In some years, few samples were collected at any ports. For these gears, we apportioned landings as follows. First, we treated all samples from market categories that might contain significant numbers of bocaccio or chilipepper as a single "super-market category" (our "mixed rockfish group" mentioned above for trawl landings). Furthermore, we did not attempt to apportion separately by quarter, instead we stratified temporally by year. When we had at least 5 samples for the year/port complex combination, we estimated proportions of the supermarket category that were bocaccio and chilipepper directly from the data for that year/port complex, weighting the samples equally.

For port complex/year combinations with fewer than 5 samples, we estimated the proportions using information from other years and locations that were more intensively sampled. We did this by developing a general linear model for proportions of bocaccio (or chilipepper), including year and region effects. To do this we first defined the regions of southern California (the port complexes of San Diego, Los Angeles, Ventura, and Santa Barbara), the port complex of Morro Bay, the port complex of Monterey, and finally all ports further north. Although we recognize that differences exist within these areas, the sampling was, in our judgement, too sparse to justify any finer stratification at this point. For each port complex, for each year, we then calculated the proportions of our super-market category that were bocaccio and chilipepper. We fit a general linear model (GLM) to the proportions, including both year and region as class variables (i.e. fixed effects), and weighting the proportions by the sample sizes used to calculate them. Thus, for poorly sampled year/port complexes (i.e. fewer than five samples), we used the predicted proportions from the GLM for the appropriate year/geographical strata as our estimates of the proportion bocaccio (or chilipepper). For set net, sample data were not available before 1982, so for 1980 and 1981 we used the least-square means for the appropriate region as our estimates of the proportions. In a few cases, the model estimated a proportion less than zero, and in these situations we used a value of zero in our calculations. The predicted and observed proportions matched reasonably well in

cases where our samples sizes exceeded 5 (Attachment Fig. 1). This observed fit, using raw proportions as the dependent variable, was better than the fit we obtained using logarithmic or logit transformations.

Our initial estimates following the above procedure indicated significant landings from the Eureka area for the hook-and-line / longline fishery. This was of some concern because it is generally known that bocaccio landings were not generally high in that area, there were very few samples from Eureka, and this area was being lumped with ports to the south in our calculations of the proportion bocaccio. To evaluate this, we examined the proportion bocaccio in Eureka and at the port complexes it was being lumped with (San Francisco, Bodega Bay, and Fort Bragg) by year for the trawl fishery, which was generally well sampled. We found that the proportion bocaccio in trawl landings at Eureka was comparable to the proportion trawl at the other port complexes through 1984, but dropped in 1985 to an average of 42.7% of the proportion seen at the other ports. Consequently we reduced the 1985-1991 hook-and-line landings in the Eureka area to 42.7% of the values estimated by the GLM model. (A similar evaluation for chilipepper found that the proportion at Eureka was 37.5% of the proportion landed at the San Francisco, Bodega Bay and Fort Bragg port complexes over the entire time series, and the landings of hook-and-line chilipepper were adjusted accordingly.)

There were also some assumptions and calculations required to generate length or age compositions from the raw data or originally provided compositions. This is because not all fish were sexed, and unsexed fish needed to be assigned to a sex. This was done based on the other data for that year. For the length-composition data, we classified the lengths into 2 cm tl groups and applied the sex ratio in their group to the unsexed fish. If none of the fish in the group were sexed, they were assigned a sex based on the sex ratios in the closest size group with available information, or the average of the closest size groups if two groups were equally close.

Assigning sexes to the age composition data was more complex because there were fish of unknown age as well as unknown sex. There were several categories of data. These included unknown sex and unknown age (USUA), unknown sex and known age (USKA), known sex and unknown age (KSUA), and known sex and age (KSKA).

First, the USUA fish were assigned an age based on the proportion of USKA fish at each age to the total USKA fish at all ages. These USUA fish were now considered to be in the USKA category. Next, the USKA fish at each age were assigned a sex based on the sex ratio in the KSKA fish at that age. The USUA fish were now considered part of the KSKA category. Finally, the KSUA fish were assigned an age based on the proportion of KSKA fish of that sex at each age to the total KSKA fish of that sex.

In the case of bocaccio hook and line in 1990 we reported the data as a combined sex length composition because a majority of the lower half of the length composition consisted of unsexed fish.

Attachment Table 1. Number of trips sampled (COUNT), and reported landings (MT) of mixed rockfish likely to contain bocaccio or chilipepper (a specified list of market categories), by CDF&G port complex (PORTGRP), year and gear type.

----- YEAR=1980 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	4	306.723
Monterey	1	240.863
San Francisco	10	87.049
Bodega Bay	0	13.345
Fort Bragg	0	39.995
Eureka	0	136.867
Santa Barbara	0	53.511
Ventura	0	177.665
Los Angeles	0	220.138
San Diego	0	91.395

----- YEAR=1980 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	0	13.132
Monterey	0	32.089
San Francisco	0	1.227
Bodega Bay	0	0.568
Santa Barbara	0	6.209
Ventura	0	16.129
Los Angeles	0	147.765
San Diego	0	15.684

----- YEAR=1980 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	43	1533.32
Monterey	45	2338.84
San Francisco	30	1854.12
Bodega Bay	0	231.23
Fort Bragg	91	1936.08
Eureka	96	5450.10
Santa Barbara	0	59.66
Ventura	0	0.04

Attachment Table 1 (cont.)

----- YEAR=1981 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	0	279.629
Monterey	0	172.201
San Francisco	0	137.157
Bodega Bay	0	21.237
Fort Bragg	0	54.626
Eureka	1	237.088
Santa Barbara	0	64.033
Ventura	0	176.817
Los Angeles	0	367.816
San Diego	0	95.237

----- YEAR=1981 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	0	1.746
Monterey	0	106.549
San Francisco	0	4.471
Bodega Bay	0	0.265
Eureka	0	0.029
Santa Barbara	0	2.386
Ventura	0	135.847
Los Angeles	0	309.403
San Diego	0	597.684

----- YEAR=1981 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	40	1324.10
Monterey	37	1689.53
San Francisco	11	1838.14
Bodega Bay	3	557.85
Fort Bragg	56	2252.19
Eureka	64	4098.93
Santa Barbara	0	92.99
Ventura	0	4.50
Los Angeles	0	0.77

Attachment Table 1 (cont.)

----- YEAR=1982 Gear type=Book -----

PORTGRP	COUNT	MT
Morro Bay	2	623.248
Monterey	2	296.308
San Francisco	0	154.552
Bodega Bay	0	28.101
Fort Bragg	0	45.458
Eureka	4	330.433
Santa Barbara	0	121.683
Ventura	0	263.489
Los Angeles	0	532.699
San Diego	0	141.576

----- YEAR=1982 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	1	182.722
Monterey	1	378.121
San Francisco	0	16.126
Bodega Bay	0	1.644
Fort Bragg	0	0.883
Santa Barbara	0	1.756
Ventura	0	51.078
Los Angeles	0	288.161
San Diego	0	605.029

----- YEAR=1982 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	33	1401.36
Monterey	85	1882.02
San Francisco	36	1544.77
Bodega Bay	9	491.41
Fort Bragg	54	1941.26
Eureka	143	1830.87
Santa Barbara	0	132.00
Ventura	0	54.93
Los Angeles	0	21.47
San Diego	0	1.40

Attachment Table 1 (cont.)

----- YEAR=1983 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	5	166.500
Monterey	1	123.343
San Francisco	0	84.700
Bodega Bay	0	13.671
Fort Bragg	0	12.071
Eureka	3	49.196
Santa Barbara	0	79.531
Ventura	0	203.975
Los Angeles	0	193.638
San Diego	0	131.365

----- YEAR=1983 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	1	38.105
Monterey	8	761.465
San Francisco	0	76.696
Bodega Bay	0	0.356
Santa Barbara	0	6.894
Ventura	0	74.985
Los Angeles	0	141.904
San Diego	0	565.705

----- YEAR=1983 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	66	936.43
Monterey	84	1353.54
San Francisco	30	1271.31
Bodega Bay	21	1871.18
Fort Bragg	130	2449.74
Eureka	165	1742.73
Santa Barbara	0	158.60
Ventura	0	6.87
Los Angeles	0	256.62
San Diego	0	0.37

Attachment Table 1 (cont.)

----- YEAR=1984 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	3	111.753
Monterey	0	18.793
San Francisco	1	39.036
Bodega Bay	0	12.864
Fort Bragg	0	3.124
Eureka	2	2.041
Santa Barbara	0	51.416
Ventura	0	97.634
Los Angeles	0	209.646
San Diego	0	121.106

----- YEAR=1984 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	8	42.981
Monterey	1	288.883
San Francisco	0	152.608
Bodega Bay	0	4.008
Santa Barbara	0	113.406
Ventura	0	96.763
Los Angeles	0	258.512
San Diego	0	468.689

----- YEAR=1984 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	95	688.07
Monterey	106	1430.53
San Francisco	44	2011.32
Bodega Bay	49	2269.37
Fort Bragg	73	1845.80
Eureka	90	1355.31
Santa Barbara	0	77.54
Ventura	0	14.38
Los Angeles	0	21.12
San Diego	0	1.24

Attachment Table 1 (cont.)

----- YEAR=1985 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	10	156.330
Monterey	0	62.447
San Francisco	0	81.602
Bodega Bay	0	44.654
Fort Bragg	0	38.941
Eureka	1	191.515
Santa Barbara	0	51.978
Ventura	0	140.233
Los Angeles	0	120.073
San Diego	0	121.096

----- YEAR=1985 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	8	156.635
Monterey	26	643.804
San Francisco	24	700.376
Bodega Bay	0	6.266
Eureka	0	0.401
Santa Barbara	0	107.159
Ventura	0	32.951
Los Angeles	0	330.691
San Diego	0	555.063

----- YEAR=1985 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	112	563.97
Monterey	121	1117.22
San Francisco	54	1171.61
Bodega Bay	42	1016.85
Fort Bragg	74	1057.67
Eureka	87	1497.23
Santa Barbara	0	32.88
Ventura	0	0.89
San Diego	0	0.47

Attachment Table 1 (cont.)

----- YEAR=1986 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	8	77.110
Monterey	0	34.555
San Francisco	0	153.012
Bodega Bay	0	192.963
Fort Bragg	0	140.147
Eureka	0	236.490
Santa Barbara	1	58.385
Ventura	40	213.090
Los Angeles	24	112.592
San Diego	53	191.384

----- YEAR=1986 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	9	354.40
Monterey	21	761.99
San Francisco	13	1069.60
Bodega Bay	0	6.27
Fort Bragg	0	0.01
Eureka	0	0.71
Santa Barbara	25	168.73
Ventura	11	39.89
Los Angeles	63	346.74
San Diego	157	577.30

----- YEAR=1986 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	67	1039.15
Monterey	85	1114.60
San Francisco	8	176.68
Bodega Bay	8	369.97
Fort Bragg	63	634.63
Eureka	74	696.64
Santa Barbara	4	57.19
Ventura	1	3.85
Los Angeles	0	0.46

Attachment Table 1 (cont.)

----- YEAR=1987 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	2	71.955
Monterey	0	76.368
San Francisco	5	216.759
Bodega Bay	0	186.269
Fort Bragg	0	106.471
Eureka	0	267.456
Santa Barbara	0	38.712
Ventura	1	164.120
Los Angeles	22	50.538
San Diego	51	128.670

----- YEAR=1987 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	18	361.34
Monterey	19	1181.49
San Francisco	9	432.21
Bodega Bay	0	1.45
Eureka	0	2.05
Santa Barbara	15	304.52
Ventura	8	242.84
Los Angeles	50	190.33
San Diego	68	321.68

----- YEAR=1987 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	56	504.84
Monterey	30	722.54
San Francisco	23	636.89
Bodega Bay	26	484.88
Fort Bragg	65	984.53
Eureka	86	2279.16
Santa Barbara	2	33.14
Ventura	4	20.77
Los Angeles	0	0.39
San Diego	0	0.48

Attachment Table 1 (cont.)

----- YEAR=1988 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	2	121.680
Monterey	2	79.485
San Francisco	0	318.329
Bodega Bay	0	189.678
Fort Bragg	0	155.611
Eureka	0	311.017
Santa Barbara	1	31.851
Ventura	8	185.558
Los Angeles	7	62.502
San Diego	21	86.866

----- YEAR=1988 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	15	486.314
Monterey	56	950.901
San Francisco	0	241.406
Bodega Bay	0	3.785
Santa Barbara	11	238.026
Ventura	1	132.606
Los Angeles	19	45.240
San Diego	27	93.497

----- YEAR=1988 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	55	884.11
Monterey	56	585.52
San Francisco	8	563.27
Bodega Bay	22	734.45
Fort Bragg	50	1076.59
Eureka	41	1227.44
Santa Barbara	1	5.15
Ventura	0	3.35
Los Angeles	0	0.01
San Diego	0	2.51

Attachment Table 1 (cont.)

----- YEAR=1989 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	1	149.204
Monterey	3	96.966
San Francisco	0	367.805
Bodega Bay	0	129.628
Fort Bragg	0	221.540
Eureka	0	395.634
Santa Barbara	0	28.514
Ventura	22	364.729
Los Angeles	27	95.920
San Diego	16	49.301

----- YEAR=1989 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	8	381.76
Monterey	135	1245.36
San Francisco	0	180.73
Bodega Bay	0	0.08
Fort Bragg	0	0.54
Santa Barbara	0	25.80
Ventura	2	236.86
Los Angeles	7	55.48
San Diego	9	45.82

----- YEAR=1989 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	41	1034.29
Monterey	76	892.47
San Francisco	6	990.57
Bodega Bay	8	819.92
Fort Bragg	51	1358.60
Eureka	39	853.89
Santa Barbara	0	11.16
Ventura	0	6.67
Los Angeles	0	0.03
San Diego	0	0.31

Attachment Table 1 (cont.)

----- YEAR=1990 Gear type=Hook -----

PORTGRP	COUNT	MT
Morro Bay	2	155.379
Monterey	12	122.112
San Francisco	2	476.090
Bodega Bay	0	119.550
Fort Bragg	0	281.110
Eureka	0	570.489
Santa Barbara	1	29.454
Ventura	2	316.122
Los Angeles	0	85.049
San Diego	7	50.459

----- YEAR=1990 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	9	361.78
Monterey	134	1065.07
San Francisco	0	235.71
Bodega Bay	0	0.29
Eureka	0	0.03
Santa Barbara	0	17.21
Ventura	0	298.85
Los Angeles	0	38.92
San Diego	10	65.82

----- YEAR=1990 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	51	760.84
Monterey	52	152.12
San Francisco	18	1668.40
Bodega Bay	16	754.15
Fort Bragg	59	1629.15
Eureka	37	1130.39
Santa Barbara	0	8.19
Ventura	0	2.57
Los Angeles	0	1.13
San Diego	0	1.40

Attachment Table 1 (cont.)

----- YEAR=1991 Gear type=Hook -----

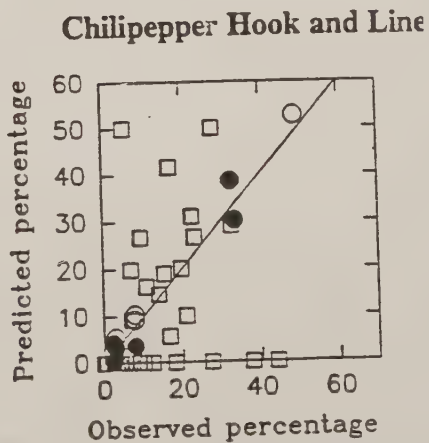
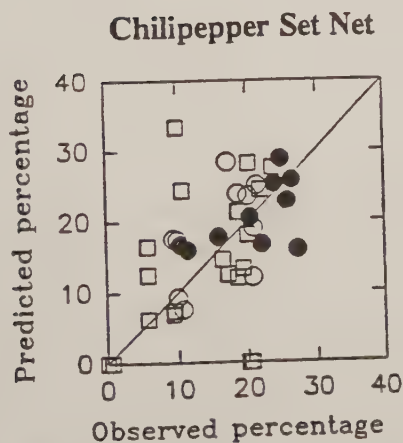
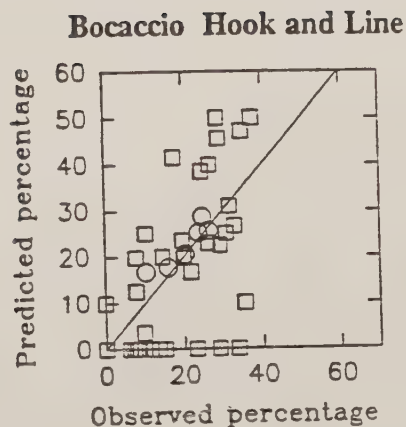
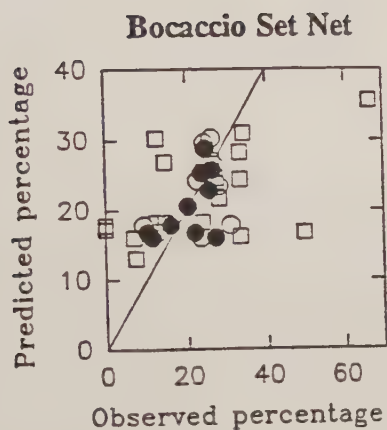
PORTGRP	COUNT	MT
Morro Bay	1	264.338
Monterey	25	273.011
Princeton	2	119.328
San Francisco	32	392.914
Bodega Bay	7	120.205
Fort Bragg	0	143.939
Eureka	0	466.350
Santa Barbara	0	42.371
Ventura	0	373.108
Los Angeles	0	124.538
San Diego	0	58.722

----- YEAR=1991 Gear type=Set net -----

PORTGRP	COUNT	MT
Morro Bay	0	119.327
Monterey	40	463.054
Princeton	2	29.172
San Francisco	5	162.146
Eureka	0	0.428
Santa Barbara	0	0.656
Ventura	0	221.948
Los Angeles	0	119.976
San Diego	0	34.708

----- YEAR=1991 Gear type=Trawl -----

PORTGRP	COUNT	MT
Morro Bay	67	640.07
Monterey	59	214.21
Princeton	17	246.14
San Francisco	33	448.81
Bodega Bay	44	504.28
Fort Bragg	46	1144.28
Eureka	24	911.84
Santa Barbara	0	4.46
Ventura	0	7.68
Los Angeles	0	1.59
San Diego	0	0.07



Attachment Figure 1. Relationship between predicted (by GLM model, see text) and directly observed proportions bocaccio and chilipepper for port complex x year combinations. Solid circles indicate observed proportions based on 25 or more sampled trips. Open circles indicate $10 \leq N < 25$, and open squares indicate $5 \leq N < 10$.

Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific

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Abstract—Ichthyoplankton and oceanographic sampling was conducted in November 1984 in waters surrounding Johnston Atoll (16°44'N, 169°32'W), a small, isolated atoll in the central Pacific Ocean. The typical flow pattern in this region is westward; the nearest island is in the Hawaiian Archipelago, 760 km away.

Most collections were dominated by oceanic taxa. In the 0–50 m stratum, larval densities were relatively uniform horizontally, but densities down-current of the island tended to be higher, and fish eggs were concentrated there. In the 50–100 m stratum, larval abundance on the down-current side of the island was markedly higher than either up-current or farther down-current. Oceanic taxa did not display this pattern, while marked areas of very high abundance characterized the island-related taxa, the most abundant including the gobiid *Eviota epiphanes* and the apogonid *Pseudamiops* sp. Estimates of geostrophic flow indicate that the region down-current of the atoll was one of return flow associated with apparent mesoscale eddies or meanders north and west of the island. This region may serve as a down-current retention area for the pelagic larvae of island-related taxa and may facilitate recruitment back to the source populations.

INTRODUCTION

THE mechanism of population maintenance in the marine fauna of islands is an important question in population biology (EHRlich, 1975; DOHERTY and WILLIAMS, 1988). Lacking an upstream source population, island species with small, pelagic larval stages must rely on local recruitment to maintain their populations despite often unidirectional ocean currents that can advect larvae away. Peculiar distributional features of larvae near islands and coral reefs have been documented in a variety of studies (LEIS and MILLER, 1976; LEIS, 1982b; SMITH *et al.*, 1987; KOBAYASHI, 1989). Several mechanisms have been proposed for the maintenance of plankton and fish larvae near islands: “winter cascading” (BODEN and KAMPA, 1953), retention in eddies remaining near islands (SALE, 1970; EMERY, 1972), flow–topography interactions and tidal features (HAMNER and HAURI, 1981; WOLANSKI and

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HAMNER, 1988) and behavioral patterns such as ontogenetic migration or epibenthic schooling (LEIS *et al.*, 1989).

The adaptive significance of pelagic larvae in tropical waters historically has been thought to be related to long-distance dispersal (BARLOW, 1981). An alternate view is that a pelagic phase with young, vulnerable life stages in offshore waters results in significantly reduced predation pressure compared to reef waters (JOHANNES, 1978). This view assumes that mortality due to advection is more than offset by the lower predation pressure in offshore waters. While early studies of tropical reef populations suggested that space availability structured communities (EHRlich, 1975), most recent papers have concluded that recruitment variability plays a major role in population dynamics, a role fundamentally similar in tropical and temperate systems (see review by DOHERTY and WILLIAMS, 1988). The spatial component of recruitment variability is relatively small compared with the large intra- and interannual component (SHULMAN, 1985). CHOAT *et al.* (1988) have suggested that the spatial variability may be a result of settlement and habitat selection, whereas temporal variability is related to specific, and often rare, oceanographic events that lead to strong recruitment for island fish fauna.

Obviously variability in advective processes is an important component of recruitment variability, particularly for maintaining a population at an isolated island. JOHANNES (1978) suggested that spawning during seasons of weakest prevailing currents and winds may help retain larvae in waters near the island, and LOBEL (1989) suggested that spawning peaks coincide with the highest prevalence of mesoscale eddies. The evidence for concentrations of larval fish coinciding with eddies or other features needed to support these arguments is equivocal. In this paper, we examine the distribution of ichthyoplankton around an isolated oceanic island and assess the distributional patterns in light of physical oceanographic conditions.

MATERIALS AND METHODS

The study site was Johnston Atoll, located at 16°44'N, 169°32'W in the central Pacific Ocean, composed of a reef with four small islands in a lagoon approximately 20 km across the long axis of its 18 m isobath. The nearest land is French Frigate Shoals, a group of small islands in the Hawaiian Archipelago, some 760 km to the north. Surveys were conducted aboard the NOAA ship *Townsend Cromwell* during November 1984.

Environmental sampling was conducted with expendable bathythermograph (XBTs, Sippican T-4) and conductivity-temperature-depth (CTD) stations. A 93 km × 93 km grid, symmetrical around the island, was developed, and XBT and CTD stations were occupied in a regular pattern in this grid. The CTD data were processed following RODEN and IRISH (1975) using algorithms from FOFONOFF and MILLARD (1983).

Ichthyoplankton was sampled at night with an opening-closing Tucker trawl (CLARKE, 1969) with three nets and a double-release mechanism operated by messengers (BOEHLERT *et al.*, 1985). Each net was 0.333 mm mesh (Nitex) with a 1.4 m² mouth. Ship speed varied between 0.9 and 1.1 m s⁻¹ to maintain a wire angle of 45°. At this angle, the effective mouth area of the net is 1.0 m². Since no time-depth recorder was available, tow depths were estimated as a function of wire angle and meters of wire out.

Samples were taken to describe both the vertical and horizontal distributions of ichthyoplankton. Four nominal depth strata (0-25, 25-50, 50-100 and 100-200 m) were initially sampled at four stations to describe the pattern of vertical distribution. An

uncontaminated, discrete-depth sample was collected in the second net by lowering the trawl with the first net open, opening the second net for the desired sampling time and then closing it. The two shallower strata were sampled in a single deployment by lowering the net to 50 m, opening the second net and then opening the third net at a depth of 25 m. For the two deeper strata, the second net was closed at the upper end of the stratum, and the trawl was retrieved with the third net open. Within each stratum, the net was fished in a stepped oblique fashion. Based upon a preliminary assessment of early sampling, larvae were most abundant in the 50–100 m stratum. Stations to determine the pattern of geographic distribution around the island were thus sampled at 0–50 and 50–100 m. The long axis of the station grid was oriented east–west in the general current flow pattern in this region (BARKLEY, 1972).

Tows were 12–24 min in duration. Water volumes filtered were estimated with a calibrated General Oceanics flowmeter mounted in the center of each net. Missing flowmeter readings were estimated using standard methods (SMITH and RICHARDSON, 1977). Plankton samples were preserved at sea in 10% buffered formalin. Displacement volumes of plankton were measured by the difference after straining plankton from a known total volume and measuring the water volume (OMORI and IKEDA, 1984).

Whole samples were sorted for fish eggs and larvae and squid larvae in the laboratory using a dissecting microscope. Larvae were identified to the lowest possible taxon following MILLER *et al.* (1979), MOSER *et al.* (1984), LEIS and RENNIS (1984) and several unpublished sources. Larvae were categorized as either yolk-sac, preflexion, flexion, postflexion, juvenile/adult or unclassified (damaged specimens that could not be classified). After analysis, specimens were stored in 5% buffered formalin.

Larvae were divided into three different types based upon the habitat occupied by the adults. "Island" larvae are taxa whose adult stages are found in association with the island. "Oceanic" larvae are those with adult stages in open ocean waters; examples are reef fishes and mesopelagic fishes, respectively. The third larval type consists of species whose adult affiliation with habitat is unclear, or are a combination of different taxa that renders the classification meaningless (e.g. categories "Anguilliformes" or "unidentified larvae").

Data analysis

Optimal estimation of ocean current field. Temperature profiles combined with mean temperature–salinity (T–S) relations from six CTD casts in the study area provided density profiles. Combining XBT observations with T–S relations yielded dynamic height profiles. Dynamic height was computed relative to 450 m.

The dynamic height data were interpolated objectively by a statistical procedure, "objective analysis", that is detailed elsewhere (GANDIN, 1965; BRETHERTON *et al.*, 1976; CARTER, 1983; SUN *et al.*, 1988). The correlation function needed by objective analysis was assumed to be in the form of

$$F(r) = \left(1 - \frac{r^2}{b^2}\right) \exp\left(-\frac{r^2}{2b^2}\right),$$

where r is the spatial interval and b is the spatial correlation scale, either a typical eddy or the first Rossby radius, R_b , in the study area (CARTER and ROBINSON, 1987). ROBINSON *et al.* (1986) determined the spatial correlation scale from dynamic height data observed in the

California Current region and fitted the correlation with the above formula. Due to the nature of our data, the determination of correlation scale from dynamic height data is not feasible. EMERY *et al.* (1984) calculated R_i from hydrocast data for 5° squares of the North Pacific. They found that the R_i values in an open ocean area near Johnston Atoll were approximately 75 km. Based upon their findings, we chose a typical correlation scale on the order of 75 km. The objectively interpolated dynamic height data were then smoothed by using a Shapiro filter of order 4 (SHAPIRO, 1970). Such filtering can remove unresolvable, small-scale features of two grid-point intervals.

Ichthyoplankton data. Egg and larval densities were standardized as number per 1000 m^3 of water filtered in each tow. Because of the non-normal distribution of ichthyoplankton data, pairwise comparisons of abundance in differing locations or depth strata were made using a randomization *t*-test (SOKAL and ROHLF, 1981) with 10,000 randomized iterations. This test requires no assumptions about the underlying distribution of the data. Geographic plots of larval abundance isopleths were made using Golden Graphics "Surfer" software; grids were developed by using kriging, and the resultant plots smoothed by cubic spline.

Assemblage groupings of fish larvae and habitats were determined with a Braun-Blanquet two-way synthesis table technique (MUELLER-DOMBOIS and BRIDGES, 1981) using the 1987 version of the COENOS program (CESKA and ROEMER, 1971). This program first rejects species with cosmopolitan distributions (those occurring in more than two-thirds of all samples). Similar species are then combined into groups based upon co-occurrence in the samples. Co-occurrence is defined by presence or absence, independent of abundance. A taxon was included in a group if the species occurred in at least 50% of the sites where that group occurred and in no more than 20% of the sites outside this group. Analysis was based upon all samples with a subset of 90 taxa, excluding very rare taxa and higher level taxa that comprise several species.

RESULTS

Oceanographic conditions

Thirty-four XBT and six CTD casts were taken over a 8650 km^2 domain (Fig. 1) during 11–12 November 1984 to describe the physical environment. Surface temperatures ranged from 27.2° to 27.6°C ; a typical temperature profile (Fig. 2) was characterized by an isothermal mixed layer of approximately 100 m depth and declining temperature with depth below the mixed layer. The mixed layer depth (as judged by the 26.8°C isotherm) varied from 60 to 106 m, and the temperature range at 100 m was 24.5° to 27.2°C .

The estimated geostrophic current field at the surface is characterized by current speeds of up to about 30 cm s^{-1} (Fig. 3A). The pattern is similar at 100 m (Fig. 3B). The geostrophic flow pattern supports the general pattern of westward flow to the east of the island, characteristic of this latitude (BARKLEY, 1972), but complexities in flow suggest either eddies or meandering wave crests near the island. Flow was eastward to the north side of the island, with the suggestion of a mesoscale cyclonic eddy at the north end of the domain (Fig. 3). The eastward return flow on the west side of the island was associated with this supposed eddy and with a feature suggestive of a mesoscale anticyclonic eddy (or meander) east-southeast of the island. A stagnant region clearly seen just off the northwest coast of the island was associated with the region of eastward (return) flow.

Larval distribution

Ichthyoplankton sampling was conducted at 44 stations on the nights of 13–21 November 1984 to describe larval fish distribution (Fig. 4). Most stations were near the atoll, although some were as far away as 38.2 km east and 65.2 km west of the island. A

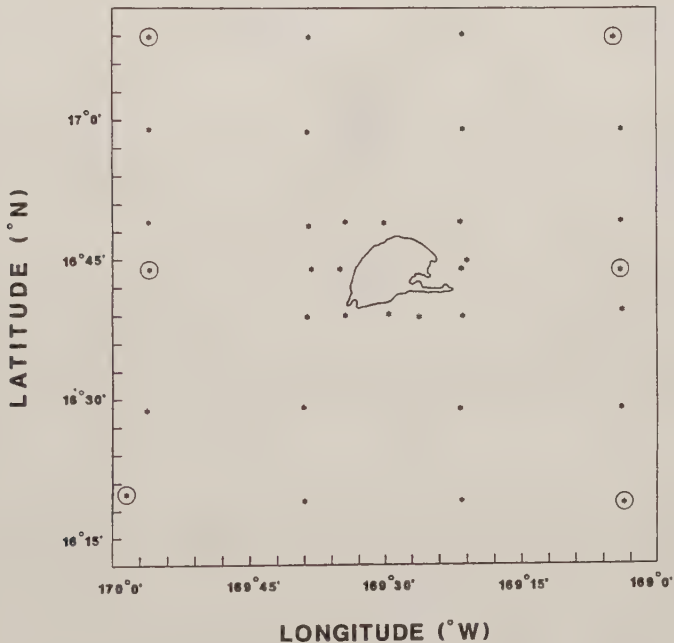


Fig. 1. Locations of 34 XBT stations (asterisks) and CTD stations (circles) around Johnston Atoll. The outline at the center indicates the 18 m isobath surrounding the atoll.

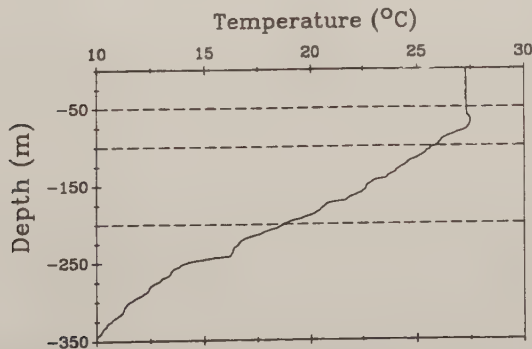


Fig. 2. Temperature profile of a typical XBT cast taken near Johnston Island. Note the extent of the isothermal mixed layer. Horizontal dashed lines indicate the boundaries of the major depth strata sampled for ichthyoplankton.

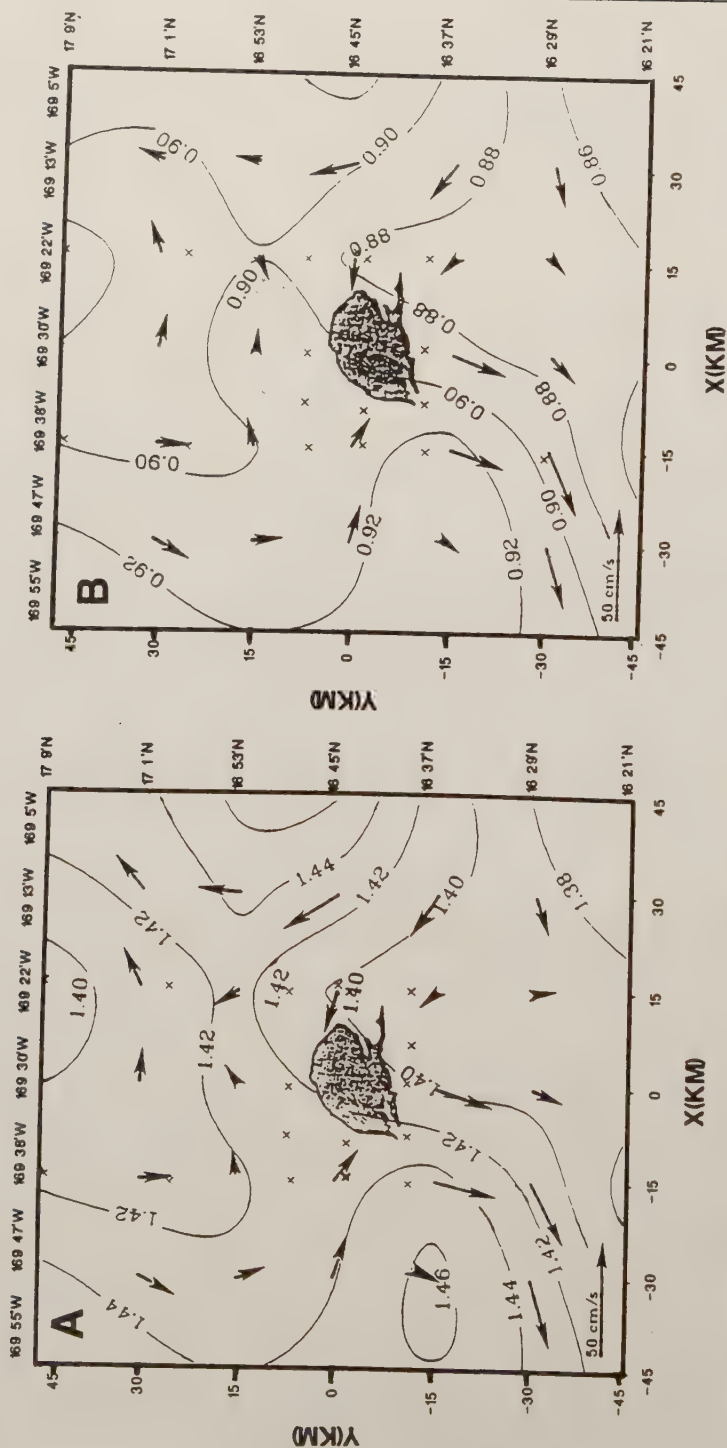


Fig. 3. Objective analysis-based quasi-geostrophic flow pattern at (A) the surface and (B) 100 m relative to 450 m. Contours are dynamic height in dyn. m. Arrows represent current vectors, arrow tails indicate the grid points where the geostrophic flows were actually computed, and their lengths represent current speed. Xs indicate XBT stations. Note that the extent of this domain is less than that in Fig. 1.

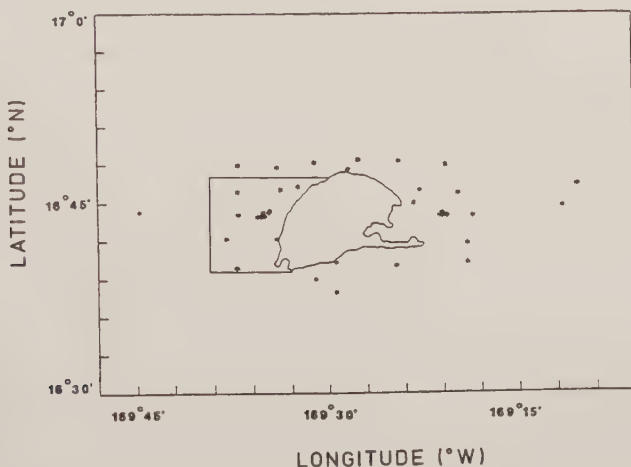


Fig. 4. Geographic locations of the 44 ichthyoplankton stations sampled around Johnston Atoll on the nights of 13–21 November 1984. In addition to those shown on the map, there are two stations farther to the west (at 16°44.0'N, 170°5.0'W and 16°44.4'N, 170°4.1'W) and two farther to the east (at 16°44.5'N, 169°52.5'W and 16°45.2'N, 169°50.5'W). The outline at the center indicates the 18 m isobath surrounding the atoll, and the box to the west of the island indicates the putative retention area used to contrast densities.

total of 8252 fish eggs, 12,777 fish larvae, 208 juvenile/adult fishes, 835 squid larvae and 2755 ml of plankton (displacement volume) were collected in 70 plankton samples. Volumes of water filtered ranged from 499 to 1477 m³ per sample (mean, 1034 m³). Fish larvae were identified to 322 taxa in 64 families and 15 orders. To facilitate analysis, these were reduced to a total of 145 taxa by combining rare or unidentified types (within families) to a higher level taxa. Numerically, the collections were dominated by myctophids (46.5% of the total; dominant species: *Bolinichthys* sp., *Ceratoscopelus warmingi* and *Diaphus* spp.), gobiids (19.0%; dominant species: *Eviota epiphanes* and *Gnatholepis anjerensis*), gonostomatids (6.0%; dominant species: *Cyclothone* spp. and *Gonostoma* spp.), photichthyids (4.7%; dominant species: *Vinciguerria nimbaria*), apogonids (4.4%; dominant species: *Pseudamiops* spp.) and paralepidids (2.8%; dominant species: *Lestidium* spp.). As a function of developmental stage, our collections took 34 yolk-sac, 6256 preflexion, 1675 flexion, 3834 postflexion, 208 juvenile/adult and 978 unclassified fishes.

Vertical distribution

Four complete stations at four depth strata (0–25, 25–50, 50–100 and 100–200 m) were occupied at two locations: about 9.5 km west (16°44'N, 169°35'W) and 16.7 km east (16°44'N, 169°21'W) of the center of the atoll. Because this early sampling revealed larvae most abundant in the 50–100 m stratum, sampling in the two shallower strata was discontinued and a single sample in the 0–50 m stratum was substituted. Later analysis of the vertical distributions in the four samples of the 0–25 and 25–50 m strata demonstrated only minor differences in the densities of larvae, specific taxa and combined categories of

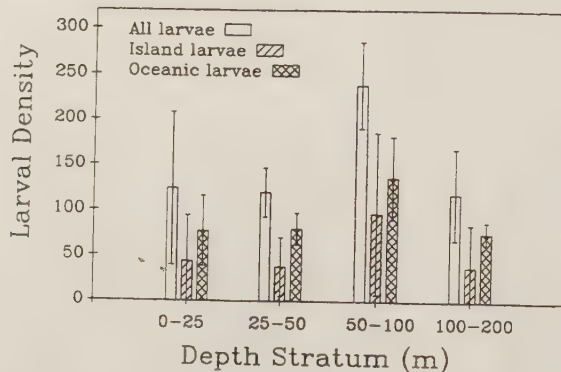


Fig. 5. Vertical distribution of larval fishes from the four stations where four depth strata were sampled. Each value of larval density (larvae 1000 m⁻³) is the mean of four samples taken at different geographic locations. Error bars represent ± 2 S.E.

larvae (Fig. 5). The two shallow strata had similar mean values for all larval classes, although variability was higher in the 0–25 m stratum. Densities were significantly higher in the 50–100 m stratum for all larvae and oceanic larvae (ANOVA, $P < 0.10$), but island larvae did not show significant differences among depths. Densities of all larval types decreased in the 100–200 m stratum to values similar to that in the shallowest stratum (Fig. 5). A more detailed analysis of vertical distribution is based upon three strata, 0–50, 50–100 and 100–200 m. The eight samples from 0–25 and 25–50 m were combined (by station) into four 0–50 m samples.

Fish larvae and eggs showed variable patterns of distribution among the depth strata (Table 1). Plankton displacement volume decreased with depth and, in the deepest stratum, was about half that of the shallowest stratum. Fish eggs and larvae are generally characterized by patchy distributions, and as expected, the variance of density was relatively high. Fish eggs were most abundant in the shallowest stratum, decreasing to about half in the 50–100 m stratum and to about 5% of the surface values in the deepest stratum. Total larval densities were similar in the two shallowest strata with slightly higher values in the 50–100 m stratum; densities in the deepest stratum were about half those in the two shallowest strata.

Mean densities of island larvae were highest in the 50–100 m stratum, but not significantly so (one-tailed randomization t -test, $P = 0.104$). Shallow and deep strata similarly did not differ. Densities of oceanic larvae in the upper two strata were similar and were significantly greater than in the deep stratum ($P < 0.001$). The variability in abundance of island larvae was much higher than that of oceanic larvae, with coefficients of variation of 1.51 and 0.30, respectively. This difference is probably due to the greater geographic variation in abundance of island larvae (see below).

The vertical distributions of individual species are characterized by differing depths of maximum density (Table 1); only the larger patterns and those for selected species will be described here. Highest densities of most gonostomatid species occurred in the deepest stratum, but *Cyclothone* spp. were most abundant in the two upper strata. Densities of most aulopiform taxa were highest in the 50–100 m stratum. The pattern for the myctophids differed by subfamily. Densities of myctophine taxa were generally highest in the

100–200 m stratum, but the two most abundant taxa (*Hygophum proximum* and *Symbolophorus evermanni*) were equally abundant in the 50–100 m stratum. Densities of most lampanyctine taxa, as exemplified by *Ceratoscopelus warmingi* and *Diaphus* spp., were highest in the 0–50 m stratum and lowest in the 100–200 m stratum.

Most island larval taxa are Perciformes, and the most frequent pattern for perciform taxa was greatest abundance in the 0–50 m stratum. The numerically dominant taxa (*Eviota epiphanes*, unidentified gobiids, *Pseudamiops* spp., *Parapercis* sp. and *Schindleria pietschmanni*), however, were most abundant in the 50–100 m stratum. Some island taxa from among several orders were most abundant in the 100–200 m stratum; these include Chlopsidae, *Apogonichthys perdis* and Callionymidae.

Vertical distribution within species varied with developmental stage. To determine these patterns, “early larvae” were defined as yolk-sac and preflexion larvae, and “late larvae” as flexion and postflexion larvae. Juvenile/adult and unclassified categories were not included in this analysis. Several species showed patterns of increasing percentages of early stage larvae with increasing water depth; examples were *Serrivomer* sp. (with only early stage larvae in deep water) and the paralepidid *Lestidium* spp. In the Myctophidae, opposite patterns were evident between the subfamilies Myctophinae and Lampanyctinae. The percentages of early stage *Symbolophorus evermanni* larvae increased significantly with depth (ANOVA on arcsin transformed data, $P < 0.001$), whereas the opposite was true for the lampanyctines *Ceratoscopelus warmingi* ($P = 0.001$) and *Diaphus* spp. ($P < 0.001$; Fig. 6A). In the Perciformes (and among island larvae in general), a pattern of decreasing percentages of early larvae with increasing depth was apparent (Fig. 6B); the

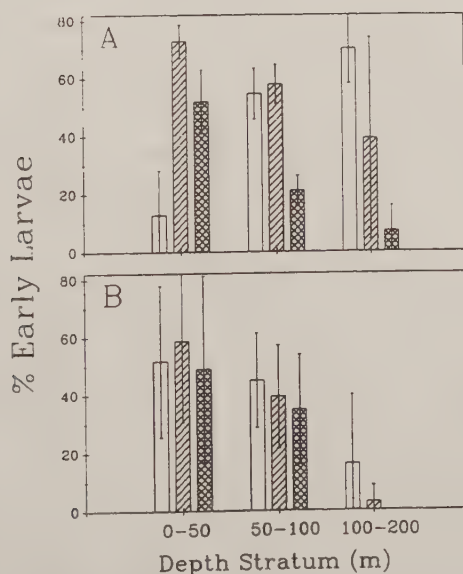


Fig. 6. Patterns of the vertical distribution of different developmental stages of six species. Percent early larvae refers to the sum of yolk-sac and preflexion larvae as a percentage of early plus late larvae (where late refers to flexion and postflexion larvae). (A) $\square$, *Symbolophorus evermanni*; ▨ , *Ceratoscopelus warmingi*; ▩ , *Diaphus* spp. (B) $\square$, *Eviota epiphanes*, *Pseudamiops* sp. and *Limnichthys donaldsoni*, respectively. Error bars represent ± 2 S.E.

Table 1. Vertical distribution of fish larvae, fish eggs, squid larvae, and plankton displacement volume around Johnston Atoll. Densities (larvae 1000 m⁻³) are mean values based upon 29, 30 and 7 samples in the 0–50, 50–100 and 100–200 m strata, respectively. Types of larvae refer to the habitat occupied by the adults, defined as island (1), oceanic (2) and other (3). Values associated with higher level taxonomic categories, such as family or higher indicate unidentified species in that category. Taxonomic categories generally follow NELSON (1984)

Taxon	Type	Larval density by stratum					
		0–50 m		50–100 m		100–200 m	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Anguilliformes	3	0.095	(0.362)	0.600	(0.917)	0.359	(0.667)
Nemichthyidae	2	0.061	(0.329)	0.000	(0.000)	0.000	(0.000)
Chlopsidae	1	0.000	(0.000)	0.053	(0.290)	0.239	(0.631)
Muraenidae	1	0.078	(0.357)	0.031	(0.167)	0.000	(0.000)
Serrivomeridae							
<i>Serrivomer</i> sp.	1	1.295	(1.519)	1.393	(1.963)	0.553	(0.734)
Congridae	1	0.041	(0.160)	0.085	(0.259)	0.000	(0.000)
Ophichthidae	1	0.094	(0.378)	0.287	(0.645)	0.122	(0.324)
Derichthyidae							
<i>Derichthys</i> sp.	2	0.000	(0.000)	0.199	(0.662)	0.000	(0.000)
Stomiiformes							
Stomioidea	2	0.596	(1.151)	1.083	(1.178)	2.081	(1.052)
Gonostomatidae	2	0.057	(0.212)	0.057	(0.217)	0.113	(0.300)
<i>Cyclothone</i> spp.	2	11.617	(5.496)	9.017	(5.434)	1.106	(1.602)
<i>Diplophos taenia</i>	2	0.538	(1.270)	0.108	(0.281)	0.219	(0.374)
<i>Gonostoma</i> spp.	2	0.000	(0.000)	0.198	(0.481)	2.202	(0.973)
<i>G. atlanticum</i>	2	0.104	(0.378)	0.429	(0.826)	2.972	(2.092)
<i>G. elongatum</i>	2	0.000	(0.000)	0.084	(0.335)	1.750	(1.899)
Photichthyidae							
<i>Ichthyococcus</i> sp.	2	0.000	(0.000)	0.000	(0.000)	0.112	(0.297)
<i>Vinciguerria nimbaria</i>	2	5.767	(3.478)	11.770	(7.597)	4.344	(3.455)
Sternoptychidae							
<i>Sternoptyx</i> sp.	2	0.000	(0.000)	0.000	(0.000)	0.816	(0.810)
<i>Valenciennellus tripunctulatus</i>	2	0.000	(0.000)	0.000	(0.000)	0.232	(0.396)
Astronesthidae	2	0.424	(0.692)	0.156	(0.325)	0.000	(0.000)
<i>Astronesthes</i> spp.	2	0.089	(0.359)	0.168	(0.563)	0.245	(0.647)
Melanostomiidae							
<i>Bathophilus</i> sp.	2	0.164	(0.484)	0.000	(0.000)	0.000	(0.000)
<i>Eustomias</i> sp.	2	0.764	(1.341)	0.288	(0.527)	0.000	(0.000)
<i>Leptostomias</i> sp.	2	0.000	(0.000)	0.086	(0.263)	0.000	(0.000)
<i>Photonectes</i> sp.	2	0.015	(0.078)	0.217	(0.510)	0.000	(0.000)
Malacosteidae	2	0.028	(0.151)	0.000	(0.000)	0.000	(0.000)
Idiacanthidae							
<i>Idiacanthus</i> sp.	2	0.000	(0.000)	0.488	(0.843)	1.630	(1.601)
Aulopiformes							
Synodontidae							
<i>Synodus</i> spp.	1	0.014	(0.078)	0.242	(0.628)	0.000	(0.000)
Scopelarchidae	2	0.027	(0.147)	0.057	(0.314)	1.732	(1.753)
<i>Benthalbella</i> sp.	2	0.000	(0.000)	0.172	(0.679)	0.238	(0.631)
<i>Scopelarchus</i> spp.	2	0.000	(0.000)	0.000	(0.000)	0.551	(0.837)
Paralepididae	2	0.674	(1.308)	0.860	(1.083)	0.782	(0.909)
Lestidiini	2	0.249	(0.587)	0.657	(1.364)	0.000	(0.000)
<i>Lestidiops</i> spp.	2	1.564	(1.559)	0.825	(1.133)	0.119	(0.316)
<i>Lestidium</i> spp.	2	0.288	(0.564)	3.609	(3.545)	2.280	(2.654)

Table 1. Continued

		Larval density by stratum					
		0-50 m		50-100 m		100-200 m	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>Aulopiformes—continued</i>							
<i>Stemonosudis macrura</i>	2	0.027	(0.147)	0.000	(0.000)	0.000	(0.000)
<i>Sudis atrox</i>	2	0.302	(0.591)	1.173	(1.330)	0.583	(0.925)
<i>Notosudidae</i>	2	0.000	(0.000)	0.027	(0.150)	0.000	(0.000)
<i>Scopelosaurus</i> spp.	2	0.199	(0.569)	0.735	(1.997)	1.673	(2.189)
<i>Evermannellidae</i>							
<i>Evermannella</i> sp.	2	1.011	(1.764)	1.021	(1.100)	0.590	(0.800)
<i>Odontostomops normalops</i>	2	0.015	(0.078)	0.237	(0.660)	0.000	(0.000)
<i>Myctophiformes</i>							
<i>Myctophidae</i>	2	4.647	(4.679)	1.614	(2.000)	1.149	(1.205)
<i>Myctophinae</i>	2	0.961	(2.476)	3.907	(2.946)	2.294	(2.460)
<i>Electrona</i> spp.	2	0.013	(0.070)	0.000	(0.000)	0.112	(0.297)
<i>Gonichthys</i> sp.	2	0.000	(0.000)	0.176	(0.433)	0.351	(0.651)
<i>Hygophum proximum</i>	2	1.016	(1.402)	10.766	(7.910)	11.725	(4.636)
<i>H. reinhardti</i>	2	0.063	(0.303)	0.412	(0.585)	0.590	(0.639)
<i>Myctophum</i> spp.	2	0.000	(0.000)	0.703	(1.415)	0.353	(0.652)
<i>M. asperum</i>	2	0.000	(0.000)	0.105	(0.343)	0.000	(0.000)
<i>M. auro lanternatum</i>	2	0.000	(0.000)	0.000	(0.000)	0.113	(0.300)
<i>Protomyctophum</i> sp.	2	0.223	(0.542)	0.353	(0.629)	0.464	(0.649)
<i>Symbolophorus evermanni</i>	2	0.877	(1.244)	8.157	(5.363)	7.317	(4.011)
<i>Centrobranchus</i> spp.	2	0.000	(0.000)	0.000	(0.000)	0.114	(0.303)
<i>Benthosema</i> spp.	2	0.000	(0.000)	0.089	(0.363)	0.000	(0.000)
<i>Lampanyctinae</i>	2	0.692	(1.309)	0.317	(0.511)	0.112	(0.297)
<i>Bolinichthys</i> spp.	2	5.623	(7.482)	4.614	(4.427)	1.136	(1.289)
<i>Ceratoscopelus warmingi</i>	2	69.253	(38.334)	39.178	(24.619)	4.903	(5.185)
<i>Diaphus</i> spp.	2	10.778	(8.945)	9.188	(5.337)	4.722	(2.890)
<i>D. pacificus</i>	2	0.445	(0.798)	2.271	(1.937)	1.626	(1.425)
<i>Lampadena</i> spp.	2	0.684	(1.401)	0.111	(0.287)	0.000	(0.000)
<i>L. urophaos</i>	2	2.820	(2.959)	1.875	(1.629)	0.113	(0.300)
<i>Lampanyctus</i> spp.	2	1.361	(2.102)	1.194	(1.030)	0.568	(0.581)
<i>L. nobilis</i>	2	4.417	(3.538)	3.072	(2.128)	0.811	(0.923)
<i>L. steinbecki</i>	2	0.777	(1.327)	1.093	(1.516)	0.652	(1.393)
<i>Lobianchia</i> sp.	2	0.000	(0.000)	0.000	(0.000)	0.239	(0.631)
<i>Taaningichthys</i> sp.	2	0.061	(0.330)	0.137	(0.376)	0.000	(0.000)
<i>Triphoturus nigrescens</i>	2	0.000	(0.000)	0.059	(0.224)	0.000	(0.000)
<i>Gadiformes</i>							
<i>Bregmacerotidae</i>							
<i>Bregmaceros</i> sp.	3	0.083	(0.348)	0.883	(1.093)	2.339	(3.108)
<i>Ophidiiformes</i>	3	0.000	(0.000)	0.109	(0.355)	0.000	(0.000)
<i>Carapidae</i>	1	0.000	(0.000)	0.063	(0.239)	0.000	(0.000)
<i>Lophiiformes</i>							
<i>Antennariidae</i>	1	0.014	(0.077)	0.000	(0.000)	0.113	(0.300)
<i>Ceratioidei</i>	2	0.000	(0.000)	0.051	(0.196)	0.000	(0.000)
<i>Caulophrynyidae</i>							
<i>Caulophryne</i> sp.	2	0.181	(0.547)	0.000	(0.000)	0.000	(0.000)
<i>Melanocetidae</i>							
<i>Melanocetus johnsoni</i>	2	0.089	(0.357)	0.139	(0.377)	0.000	(0.000)

Table 1. *Continued*

Taxon	Type	Larval density by stratum					
		0-50 m		50-100 m		100-200 m	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Cyprinodontiformes							
Exocoetidae	2	0.107	(0.341)	0.031	(0.171)	0.000	(0.000)
<i>Paraxocoetus</i> sp.	2	0.075	(0.335)	0.060	(0.228)	0.000	(0.000)
Hemiramphidae	3	0.121	(0.451)	0.000	(0.000)	0.000	(0.000)
Lampriformes							
Lampridae							
<i>Lampris guttatus</i>	2	0.000	(0.000)	0.028	(0.154)	0.000	(0.000)
Mirapinnidae							
<i>Parataeniophorus</i> sp.	2	0.028	(0.151)	0.000	(0.000)	0.000	(0.000)
Beryciformes							
Melamphidae	2	0.000	(0.000)	0.028	(0.154)	0.112	(0.297)
<i>Melamphaes</i> spp.	2	0.061	(0.326)	1.254	(1.470)	0.925	(0.968)
<i>Scopelogadus</i> spp.	2	0.000	(0.000)	0.029	(0.157)	0.352	(0.652)
Holocentridae	1	1.021	(2.641)	0.000	(0.000)	0.000	(0.000)
Syngnathiformes							
Aulostomidae							
<i>Aulostomus chinensis</i>	1	0.199	(0.596)	0.000	(0.000)	0.000	(0.000)
Syngnathidae	1	0.015	(0.078)	0.150	(0.409)	0.000	(0.000)
Scorpaeniformes							
Scorpaenidae	1	0.151	(0.474)	0.237	(0.524)	0.000	(0.000)
Perciformes							
Percoidei	1	0.705	(1.259)	0.208	(0.503)	0.234	(0.399)
<i>Incertae sedis</i>							
<i>Howella</i> sp.	2	0.056	(0.302)	0.838	(1.202)	0.242	(0.412)
Serranidae	1	0.193	(0.579)	0.000	(0.000)	0.000	(0.000)
<i>Pseudogramma polyacantha</i>	1	0.000	(0.000)	0.031	(0.167)	0.000	(0.000)
Priacanthidae	1	0.029	(0.156)	0.000	(0.000)	0.000	(0.000)
Apogonidae	1	1.522	(2.224)	0.519	(0.917)	0.112	(0.297)
Apogoninae	1	1.169	(2.260)	0.991	(1.337)	0.332	(0.415)
<i>Apogonichthys perdx</i>	1	0.000	(0.000)	0.057	(0.219)	0.112	(0.297)
Epigoninae							
<i>Epigonus</i> sp.	3	1.071	(2.421)	0.246	(0.701)	0.000	(0.000)
Pseudamiinae	1	0.374	(1.055)	0.241	(0.584)	0.000	(0.000)
<i>Pseudamiops</i> spp.	1	4.764	(9.996)	6.463	(13.400)	2.063	(2.081)
Echeneidae	2	0.000	(0.000)	0.063	(0.343)	0.000	(0.000)
Carangidae							
<i>Selar crumenophthalmus</i>	1	0.094	(0.285)	0.046	(0.180)	0.000	(0.000)
Coryphaenidae							
<i>Coryphaena hippurus</i>	2	0.276	(0.640)	0.057	(0.217)	0.000	(0.000)
Bramidae							
<i>Brama</i> sp.	2	0.231	(0.610)	0.168	(0.344)	0.245	(0.647)
Mullidae	1	0.194	(0.503)	0.174	(0.474)	0.000	(0.000)
Chaetodontidae	1	0.662	(1.943)	0.000	(0.000)	0.000	(0.000)
Pomacanthidae	1	0.065	(0.352)	0.134	(0.430)	0.000	(0.000)
Pomacentridae	1	1.565	(2.759)	0.566	(1.216)	0.119	(0.316)
<i>Chromis</i> sp.	1	1.479	(2.605)	0.316	(0.527)	0.000	(0.000)

Table 1. Continued

Taxon	Type	Larval density by stratum					
		0-50 m		50-100 m		100-200 m	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Labridae	1	1.119	(2.664)	0.716	(1.051)	0.227	(0.387)
Scaridae	1	0.167	(0.482)	0.116	(0.303)	0.000	(0.000)
Chiasmodontidae	2	0.442	(0.772)	0.370	(0.659)	0.229	(0.392)
<i>Kali</i> sp.	2	0.042	(0.165)	0.083	(0.253)	0.000	(0.000)
Mugiloididae							
<i>Parapercis</i> sp.	1	0.361	(0.859)	3.272	(7.347)	1.253	(1.990)
Creediidae							
<i>Limnichthys donaldsoni</i>	1	1.243	(2.492)	1.950	(3.308)	1.145	(1.347)
Champsodontidae							
<i>Champsodon</i> sp.	1	0.000	(0.000)	0.057	(0.310)	0.000	(0.000)
Blenniidae							
<i>Istiblennius gibbifrons</i>	1	0.248	(0.592)	0.176	(0.550)	0.114	(0.303)
Salariai	1	4.234	(8.840)	2.936	(5.422)	0.119	(0.316)
Schindleriidae	1	0.197	(0.986)	0.295	(0.834)	0.113	(0.300)
<i>Schindleria pietschmanni</i>	1	0.978	(2.693)	2.852	(5.404)	0.465	(0.635)
<i>S. praematura</i>	1	1.447	(3.464)	0.808	(1.508)	0.122	(0.324)
Callionymidae	1	0.000	(0.000)	0.205	(0.447)	1.258	(1.941)
Gobiidae	1	8.688	(13.538)	20.944	(44.699)	4.534	(5.337)
<i>Eviota epiphanes</i>	1	8.885	(23.729)	35.334	(95.775)	12.502	(26.771)
<i>Gnatholepis anjerensis</i>	1	0.497	(1.858)	0.202	(0.593)	0.000	(0.000)
Acanthuridae	1	0.359	(1.021)	0.186	(0.414)	0.000	(0.000)
Scombroidei	2	0.095	(0.350)	0.186	(0.560)	0.000	(0.000)
Scombrabrachidae							
<i>Scombrabrach heterolepis</i>	2	2.672	(2.742)	0.552	(0.900)	0.245	(0.647)
Gempylidae							
<i>Gempylus serpens</i>	2	1.307	(1.887)	0.708	(1.775)	0.226	(0.386)
<i>Lepidocybium flavobrunneum</i>	2	0.176	(0.734)	0.038	(0.161)	0.000	(0.000)
<i>Nealotus tripes</i>	2	0.208	(0.582)	0.031	(0.171)	0.000	(0.000)
<i>Nesiarchus nasutus</i>	2	0.213	(0.555)	0.188	(0.456)	0.000	(0.000)
Trichiuridae							
<i>Lepidopus</i> sp.	2	0.000	(0.000)	0.000	(0.000)	0.119	(0.316)
Scombridae	2	0.098	(0.340)	0.058	(0.223)	0.226	(0.386)
<i>Katsuwonis pelamis</i>	2	1.756	(1.692)	0.205	(0.805)	0.114	(0.303)
<i>Scomber japonicus</i>	2	0.042	(0.166)	0.000	(0.000)	0.000	(0.000)
<i>Thunnus</i> spp.	2	0.115	(0.390)	0.046	(0.183)	0.000	(0.000)
Istiophoridae	2	0.028	(0.151)	0.000	(0.000)	0.000	(0.000)
Nomeidae							
<i>Cubiceps baxteri</i>	2	0.206	(0.472)	0.069	(0.220)	0.000	(0.000)
<i>C. pauciradiatus</i>	2	0.105	(0.373)	0.141	(0.391)	0.000	(0.000)
Pleuronectiformes							
Bothidae	1	0.014	(0.078)	0.088	(0.362)	0.000	(0.000)
Tetraodontiformes							
Balistoidei	1	0.000	(0.000)	0.031	(0.172)	0.000	(0.000)
Monacanthidae	1	0.014	(0.078)	0.000	(0.000)	0.000	(0.000)
Ostraciidae	1	0.000	(0.000)	0.112	(0.362)	0.000	(0.000)
Tetraodontidae	1	0.014	(0.078)	0.113	(0.361)	0.000	(0.000)

Table 1. *Continued*

Taxon	Type	Larval density by stratum					
		0-50 m		50-100 m		100-200 m	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Unidentified larvae	3	2.884	(2.954)	3.378	(4.255)	1.049	(0.767)
Island larvae		42.911	(52.490)	81.280	(151.190)	25.299	(36.786)
Oceanic larvae		139.197	(56.525)	129.927	(40.956)	69.424	(11.837)
Total larvae		186.361	(77.521)	216.430	(151.870)	98.470	(43.262)
Fish eggs		180.224	(540.891)	93.047	(238.143)	8.700	(7.578)
Squid larvae		14.890	(7.042)	9.274	(7.203)	5.737	(4.432)
Plankton (ml 1000 m ⁻³)		43.010	(11.805)	33.897	(10.028)	19.571	(5.041)

trend was significant for *Pseudamiops* sp. ($P = 0.05$) and *Limnichthys donaldsoni* ($P < 0.10$) but not for *Eviota epiphanes* ($P = 0.263$).

Geographic distribution

The results of the objective analysis suggested an area of return flow on the west-northwest side of the island; such an area might serve to retain island larvae for later recruitment. Indeed, certain categories of larvae were more abundant there. Sufficient samples existed in the 0-50 and 50-100 m strata to allow a geographic analysis of distribution. In the 0-50 m stratum, fish eggs were concentrated in this area (Fig. 7A), with the maximum recorded density more than five times that of the mean density (Table 1). Total fish larvae showed a pattern of slightly higher densities near this region as well as off the east-northeast side of the island (Fig. 7B). No clear pattern was discernible for oceanic larvae (Fig. 7C); island larvae, on the other hand, were concentrated in the return flow region but were in very low abundance elsewhere (Fig. 7D). Neither squid larvae nor plankton displacement volume increased in abundance in this region.

The patterns in the 50-100 m stratum (Fig. 8) were more pronounced than those in the shallower stratum. Mean densities of fish eggs were much lower in the 50-100 m stratum (Table 1), but densities in the area just downstream of the island were high, decreasing with increasing distance from the island to near zero (Fig. 8A). Superimposed upon a mean background density of about 150 larvae 1000 m⁻³, total larval densities were also much greater in this area (Fig. 8B). Similar to the situation in the 0-50 m stratum, oceanic fish larvae were not concentrated in this area (Fig. 8C), but the island fish larvae were (Fig. 8D). Similar to the fish eggs at this depth (Fig. 8A), densities of island fish larvae were near zero in waters distant from the island (Fig. 8D).

To compare statistically densities in the putative downstream "retention area" with densities in other samples, an area was defined (shown bounded by the box in Fig. 4), and densities in that area were compared with densities from all other samples for selected taxa (Table 2). Fish larvae were significantly more abundant in this area ($P < 0.01$), as would be expected from Figs 7 and 8; the increase is attributable to island larvae. Fish eggs were significantly more abundant in this area in the deeper stratum ($P < 0.05$) but not in the shallow stratum, perhaps due to patchiness, as a single sample outside the area but near the

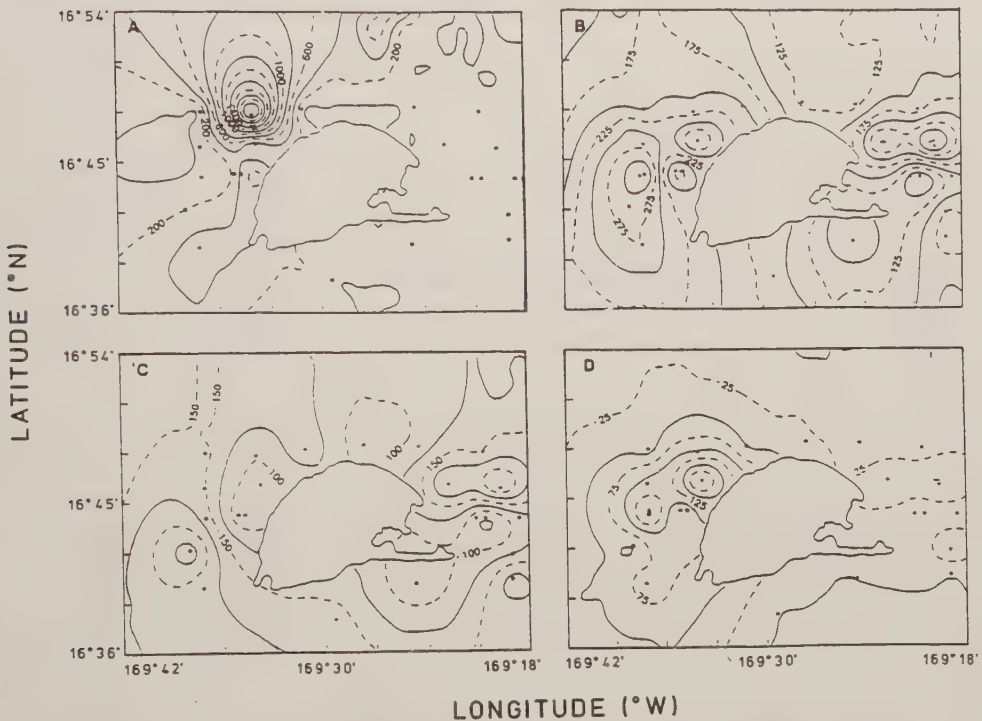


Fig. 7. Geographic patterns of density (nos 1000 m^{-3}) of (A) fish eggs, (B) total fish larvae, (C) oceanic fish larvae and (D) island fish larvae in the 0–50 m depth stratum. The outline area without contours represents the 18 m isobath surrounding Johnston Atoll.

island had 2823 fish eggs 1000 m^{-3} . Squid larvae were significantly more abundant outside the area in the shallow stratum ($P < 0.05$), and plankton displacement volume was significantly higher inside the area in the deeper stratum ($P < 0.05$).

A pattern of offshore distribution, with greater densities outside the area of return flow, was evident for many oceanic species, as exemplified by *Vinciguerria nimbaria* in both strata and *Hygophum proximum*, *Scombrolabrax heterolepis* and *Gempylus serpens* in the shallow stratum. *Scopelosaurus* spp., both species of evermannellids, *Brama* sp. and the other two gempylids also showed a trend toward greater densities outside the marked area. Among the myctophids, *Lampanyctus steinbecki* and *Lampanyctus* spp. demonstrated this offshore pattern in the deeper stratum, but the more abundant *L. nobilis* was distributed evenly. A similar discrepancy was also evident in the genus *Lampadena*, with a general trend of higher abundance outside the area but significantly higher abundance inside for *L. urophaos* in the deeper stratum ($P < 0.05$).

A trend of greater abundance of island larvae in the area of return flow is apparent, but many are not significantly more abundant because of low numbers or patchy distributions. The most abundant island taxa, however, generally were significantly more abundant in the retention area; specific cases are the Apogoninae, *Pseudamiops* spp., Labridae, *Parapercis* sp., *Limnichthys donaldsoni*, salariine blenniids, both schindleriid species,

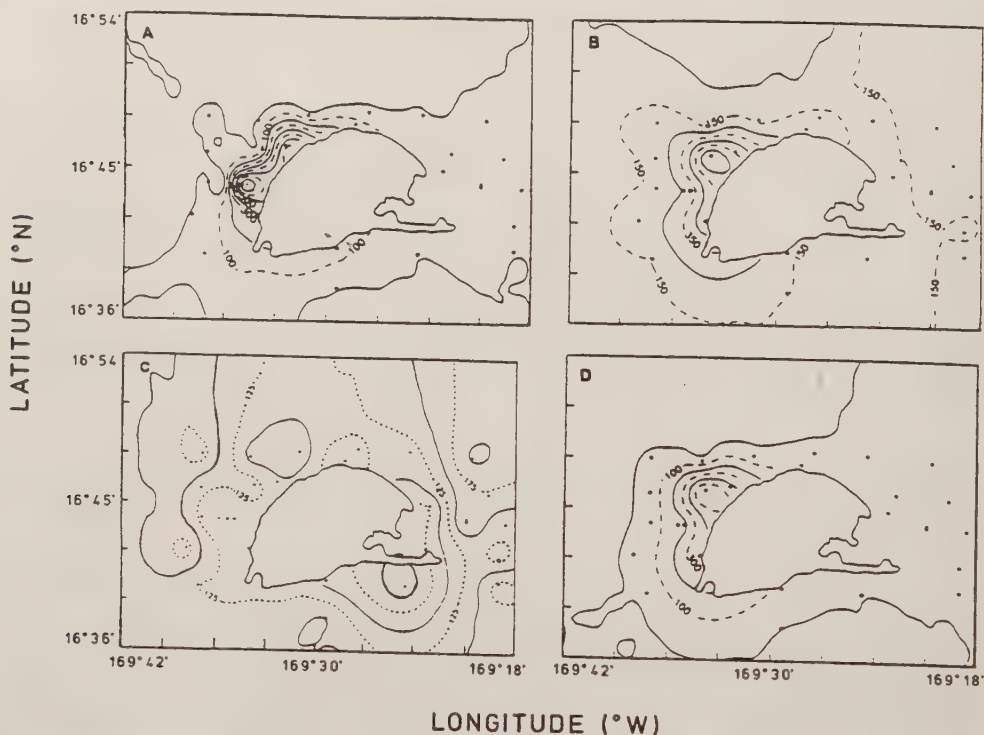


Fig. 8. Geographic patterns of densities (nos 1000 m^{-3}) of (A) fish eggs, (B) all fish larvae, (C) oceanic fish larvae and (D) island fish larvae in the 50–100 m depth stratum. The outline area without contours represents the 18 m isobath surrounding Johnston Atoll.

Eviota epiphanes and *Gnatholepis anjerensis*. The most abundant myctophid, *Ceratoscopelus warmingi*, was significantly more abundant in this area ($P < 0.05$), but only in the shallow stratum.

Species assemblages

Assemblage analysis using the two-way synthesis table defined nine assemblages of larvae with 33 taxa, of which 20 were oceanic (Table 3). These assemblages were associated with different habitats partitioned by depth and relation to the island retention area, and generally confirmed the island and oceanic groupings discussed earlier. Nine taxa were present in more than two-thirds of the samples and thus not included in the analysis; most other taxa, including both abundant and rare species, were not group members for lack of coherent distributional patterns. Group 1 comprised six island taxa abundant in all depths, but most abundant in the "island" area as opposed to the more distant samples. The occurrences of this group outside the "island" region were to the north and east in waters near the island. Group 2 comprised four abundant, oceanic, mid-water taxa (two paralepidid genera, one evermannellid and one myctophid), with wide distributions but greater abundance in the two deeper strata. Taxa in these two groups

Table 2. Mean densities (larvae 1000 m^{-3}) of selected taxa as a function of depth and location. Location 1 is bounded by the island platform to the east ($169^{\circ}32.0'W$) to $169^{\circ}38.0'$ to the west, and by $16^{\circ}39.5'N$ to $16^{\circ}46.5'N$ as shown on Fig. 4. Types of larvae refer to the habitat occupied by the adults, defined as island (1), oceanic (2) and other (3). Values associated with higher level taxonomic categories, such as family or order, indicate unidentified species in that category. Densities of selected taxa were compared within depth zones if at least 20 larvae of that taxon were captured at that depth. Significantly higher densities are indicated (one-tailed randomization tests; * $P < 0.05$; ** $P < 0.01$; not corrected for multiple testing)

Taxon	Type	Density at depth 0–50 m				Density at depth 50–100 m			
		Location 1		Location 2		Location 1		Location 2	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Anguilliformes									
Serrivomeridae									
<i>Serrivomer</i> sp.	2	0.811	(1.018)	1.449	(1.636)	2.592*	(3.228)	0.879	(0.703)
Ophichthidae	1	0.120	(0.317)	0.086	(0.402)	0.473	(0.951)	0.207	(0.469)
Stomiiformes									
Gonostomatidae									
<i>Cyclothone</i> spp.	2	10.990	(5.591)	11.816	(5.583)	11.031	(5.271)	8.153	(5.393)
<i>Diplophos taenia</i>	2	0.119	(0.204)	0.671	(1.436)	0.177	(0.353)	0.078	(0.248)
Photichthyidae									
<i>Vinciguerrina nimbaria</i>	2	3.083	(2.063)	6.621**	(3.427)	7.141	(5.134)	13.754**	(7.706)
Astronesthidae									
<i>Astronesthes</i> spp.	2	0.000	(0.000)	0.118	(0.411)	0.000	(0.000)	0.240	(0.664)
Melanostomatidae									
<i>Eustomias</i> sp.	2	0.778	(1.441)	0.760	(1.344)	0.289	(0.434)	0.288	(0.573)
<i>Photoneustes</i> sp.	2	0.000	(0.000)	0.019	(0.090)	0.000	(0.000)	0.310	(0.588)
Idiacanthidae									
<i>Idiacanthus</i> sp.	2	0.000	(0.000)	0.000	(0.000)	0.293	(0.647)	0.571	(0.916)
Aulopiformes									
Synodontidae									
<i>Synodus</i> spp.	1	0.060	(0.159)	0.000	(0.000)	0.712	(0.992)	0.041	(0.188)
Paralepididae									
<i>Lestidiini</i>	2	0.000	(0.000)	0.328	(0.658)	1.397*	(2.185)	0.339	(0.660)
<i>Lestidiops</i> spp.	2	1.037	(1.147)	1.731	(1.656)	0.800	(1.163)	0.836	(1.148)
<i>Lestidium</i> spp.	2	0.560	(0.828)	0.201	(0.443)	4.216	(3.744)	3.348	(3.518)
Notosuididae									
<i>Scopelosaurus</i> spp.	2	0.000	(0.000)	0.263	(0.644)	0.000	(0.000)	1.050	(2.331)

Table 2. *Continued*

Taxon	Type	Density at depth 0-50 m				Density at depth 50-100 m			
		Location 1		Location 2		Location 1		Location 2	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>Aulopiformes—continued</i>									
<i>Evermannellidae</i>									
<i>Evermannella</i> sp.	2	0.311	(0.659)	1.234	(1.952)	0.733	(1.113)	1.144	(1.098)
<i>Odonostomops normalops</i>	2	0.000	(0.000)	0.019	(0.090)	0.000	(0.000)	0.338	(0.771)
<i>Myctophiformes</i>									
<i>Myctophidae</i>									
<i>Myctophinae</i>									
<i>Hygophum proximum</i>	2	0.119	(0.314)	1.302**	(1.496)	10.480	(9.454)	10.888	(7.411)
<i>Symbolophorus evermanni</i>	2	0.367	(0.679)	1.040	(1.348)	6.452	(4.561)	8.887	(5.614)
<i>Lampanyctinae</i>									
<i>Ceratoscopelus warmingi</i>	2	93.139*	(47.623)	61.653	(32.568)	39.323	(27.508)	39.116	(24.004)
<i>Diaphus pacificus</i>	2	0.000	(0.000)	0.586	(0.873)	1.696	(1.634)	2.518	(2.039)
<i>Diaphus</i> spp.	2	5.744	(5.078)	12.379*	(9.390)	9.084	(6.813)	9.233	(4.768)
<i>Lampadena</i> spp.	2	0.248	(0.657)	0.823	(1.553)	0.000	(0.000)	0.158	(0.334)
<i>L. urophaos</i>	2	1.967	(1.553)	3.092	(3.265)	2.901*	(1.606)	1.435	(1.463)
<i>Lampanyctus</i> spp.	2	0.556	(1.297)	1.617	(2.264)	0.665	(0.730)	1.421*	(1.071)
<i>L. nobilis</i>	2	3.567	(2.656)	4.687	(3.789)	3.060	(2.273)	3.077	(2.122)
<i>L. steinbecki</i>	2	0.323	(0.689)	0.922	(1.457)	0.386	(0.615)	1.396*	(1.691)
<i>Beryciformes</i>									
<i>Holocentridae</i>									
<i>Scorpaeniformes</i>	1	0.745	(1.971)	1.109	(2.856)	0.000	(0.000)	0.000	(0.000)
<i>Scorpaenidae</i>									
<i>Perciformes</i>	1	0.368	(0.680)	0.082	(0.382)	0.000	(0.000)	0.338	(0.602)
<i>Incertae cedis</i>									
<i>Howella</i> sp.									
<i>Priacanthidae</i>	2	0.000	(0.000)	0.074	(0.346)	0.945	(1.388)	0.791	(1.148)
<i>Apogonidae</i>	1	0.120	(0.317)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
<i>Apogoninae</i>	1	1.915	(2.145)	1.397	(2.283)	0.739	(1.204)	0.424	(0.780)
<i>Apogonichthys perdis</i>	1	3.279**	(2.812)	0.497	(1.610)	1.841*	(1.822)	0.627	(0.894)
<i>Epigoninae</i>	1	0.000	(0.000)	0.000	(0.000)	0.192	(0.381)	0.000	(0.000)
<i>Epigonus</i> sp.	3	0.796	(1.417)	1.158	(2.685)	0.195	(0.389)	0.268	(0.807)

Table 2. Continued

Taxon	Type	Density at depth 0-50 m				Density at depth 50-100 m			
		Location 1		Location 2		Location 1		Location 2	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Apogonidae—continued									
Pseudamiinae									
<i>Pseudamiops</i> spp.	1	13.616**	(16.685)	1.947	(4.388)	16.930**	(21.425)	1.977	(2.512)
Coryphaenidae	2	0.248	(0.657)	0.285	(0.651)	0.000	(0.000)	0.081	(0.257)
<i>Coryphaena hippurus</i>									
Bramidae	2	0.000	(0.000)	0.305	(0.687)	0.000	(0.000)	0.240	(0.391)
<i>Brama</i> sp.	1	0.000	(0.000)	0.256	(0.566)	0.294	(0.612)	0.123	(0.408)
Mullidae	1	0.808	(1.341)	0.616	(2.123)	0.000	(0.000)	0.000	(0.000)
Chaetodontidae	1	0.000	(0.000)	0.086	(0.404)	0.083	(0.250)	0.156	(0.492)
Pomacanthidae	1	0.000	(0.000)	1.386	(2.976)	1.034	(1.964)	0.366	(0.678)
Pomacentridae	1	2.128	(2.013)	1.490	(2.563)	0.298	(0.448)	0.324	(0.567)
<i>Chromis</i> sp.	1	1.446	(2.947)	0.823	(1.811)	1.311*	(1.386)	0.461	(0.778)
Labridae	1	2.049	(4.507)	0.823	(1.811)	1.311*	(1.386)	0.461	(0.778)
Scaridae	1	0.427	(0.660)	0.084	(0.395)	0.292	(0.442)	0.041	(0.188)
Mugiloididae									
<i>Parapercis</i> sp.	1	0.619	(0.795)	0.279	(0.879)	8.575**	(12.030)	0.999	(1.515)
Creedidae									
<i>Linnichthys donaldsoni</i>	1	3.454**	(3.869)	0.539	(1.363)	3.950*	(5.120)	1.094	(1.677)
Champsodontidae									
<i>Champsodon</i> sp.	1	0.000	(0.000)	0.000	(0.000)	0.189	(0.566)	0.000	(0.000)
Blenniidae									
<i>Isiblenius gibbifrons</i>	1	0.743	(0.793)	0.090	(0.424)	0.587	(0.909)	0.000	(0.000)
<i>Salarini</i>	1	5.055	(3.268)	3.973	(10.042)	6.221*	(8.439)	1.528	(2.685)
Schindleriidae									
<i>Schindleria pietschmanni</i>	1	3.615**	(4.735)	0.139	(0.456)	7.926**	(7.772)	0.677	(1.273)
<i>S. praematura</i>	1	5.696**	(5.248)	0.095	(0.445)	2.267**	(2.107)	0.183	(0.390)
Gobiidae									
<i>Eviota epiphanes</i>	1	35.578**	(39.096)	0.393	(0.990)	103.523**	(159.507)	6.110	(11.596)
<i>Gnatholepis anjerensis</i>	1	2.058	(3.516)	0.000	(0.000)	0.293	(0.636)	0.163	(0.585)
Acanthuridae	1	0.000	(0.000)	0.474	(1.154)	0.174	(0.346)	0.191	(0.448)

Table 2. *Continued*

Taxon	Type	Density at depth 0-50 m				Density at depth 50-100 m			
		Location 1		Location 2		Location 1		Location 2	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Perciformes—continued									
Scombrolabracidae									
<i>Scombrolabrax heterolepis</i>	2	0.811	(0.895)	3.264**	(2.877)	0.568	(0.841)	0.546	(0.945)
Gempylidae									
<i>Gempylus serpens</i>	2	0.179	(0.330)	1.665*	(2.040)	0.480	(0.770)	0.806	(2.073)
<i>Lepidocybium flavobrunneum</i>	2	0.000	(0.000)	0.232	(0.839)	0.000	(0.000)	0.054	(0.192)
<i>Nesiarchus nasutus</i>	2	0.000	(0.000)	0.281	(0.626)	0.083	(0.250)	0.234	(0.519)
Scombridae									
<i>Katsuwonis pelamis</i>	2	1.763	(2.014)	1.754	(1.630)	0.000	(0.000)	0.294	(0.955)
<i>Thunnus</i> spp.	2	0.312	(0.661)	0.053	(0.248)	0.000	(0.000)	0.065	(0.218)
Pleuronectiformes									
Bothidae	1	0.060	(0.159)	0.000	(0.000)	0.295	(0.638)	0.000	(0.000)
Island larvae		110.387**	(57.711)	21.442	(26.862)	219.682**	(226.529)	21.976	(17.490)
Oceanic larvae		142.030	(60.229)	138.296	(56.746)	123.166	(29.007)	132.824	(45.456)
Total larvae		258.580**	(67.359)	163.380	(66.517)	348.496**	(225.529)	159.830	(44.462)
Fish eggs		261.329	(317.618)	154.418	(598.641)	250.456*	(399.914)	25.586	(48.284)
Squid larvae		11.000	(4.690)	16.132*	(7.286)	8.444	(6.226)	9.629	(7.547)
Plankton (ml 1000 m ⁻³)		41.857	(16.112)	43.377	(10.538)	40.578*	(9.915)	31.033	(8.821)

Table 3. Per cent occurrence and abundance of species groups within selected depth strata and area. The species groups are those determined in the two-way synthesis table technique (see Materials and Methods). The first row of numbers in each group refers to the percentage of stations in the particular depth stratum and area in which the species assemblage occurred. The second and third rows refer to the mean and standard deviation of the combined densities (larvae 1000 m⁻³) of group taxa. Nine taxa (*Ceratoscopelus warmingi*, *Vinciguerria nimbaria*, *Diaphus spp.*, *Cyclothone spp.*, *Lampanyctus nobilis*, *Bolinichthys spp.*, *Symbolophorus evermanni*, *Hygophum proximum* and *Lampadena urophaos*) were present in more than two-thirds of the samples and thus not included in the analysis. Several other abundant species were not characterized by distributions coherent with other groups

Group no.	Species	0-50 m		50-100 m		100-200 m
		Island	Other	Island	Other	All
1	<i>Eviota epiphanes</i>					
	Salarini	100.0	21.1	100.0	44.4	57.1
	<i>Limnichthys donaldsoni</i>	50.369	6.140	131.506	10.991	15.710
	<i>Parapercis</i> sp.	(37.564)	(12.160)	(172.870)	(12.379)	(28.781)
	<i>Schindleria pietschmanni</i>					
2	Labridae					
	<i>Lestidium</i> spp.					
	<i>Diaphus pacificus</i>	28.6	26.3	77.8	94.4	71.4
	<i>Sudis atrox</i>	1.182	2.372	7.570	8.284	5.080
	<i>Evermannella</i> sp.	(1.918)	(2.644)	(5.657)	(5.588)	(2.789)
3	<i>Epigonus</i> sp.					
	Scaridae	28.6	15.8	11.1	0.0	0.0
	Chaetodontidae	2.344	2.216	0.592	0.327	0.000
	<i>Nealotus tripes</i>	(3.034)	(5.497)	(0.929)	(0.874)	
	<i>Coryphaena hippurus</i>					
4	<i>Cubiceps caeruleus</i>	14.3	21.1	0.0	0.0	0.0
	<i>Bathophilis</i> sp.	0.497	1.016	0.000	0.187	0.000
	<i>Caulophyrne</i> sp.	(1.314)	(1.853)		(0.361)	
	<i>Synodus</i> spp.	14.3	0.0	22.2	0.0	0.0
	Bothidae	0.120	0.000	1.007	0.048	0.000
5		(0.317)		(1.228)	(0.203)	
	<i>Selar crumenophthalmus</i>	14.3	0.0	22.2	5.6	0.0
	Tetraodontidae	0.180	0.042	0.473	0.094	0.112
	<i>Apogonichthys perdix</i>	(0.476)	(0.184)	(0.950)	(0.397)	(0.297)
	<i>Melamphaes</i> spp.					
6	<i>Bregmaceros</i> sp.	0.0	5.3	85.7	72.2	57.1
	<i>Howella</i> sp.	0.514	0.171	2.527	3.972	4.096
	<i>Hygophum reinhardtii</i>	(0.879)	(0.745)	(2.123)	(2.847)	(4.160)
	<i>Idiacanthus</i> sp.	0.0	0.0	22.2	22.2	100.0
	<i>Gonostoma atlanticum</i>	0.000	0.142	0.782	1.212	6.805
7	<i>Gonostoma</i> spp.		(0.461)	(1.568)	(1.939)	(3.012)
	<i>Scopelosaurus</i> spp.	0	0	0	5.6	42.9
	<i>Gonostoma elongatum</i>	0.000	0.142	0.000	0.634	3.974
	<i>Scopelarchus</i> spp.		(0.463)		(1.738)	3.232

approached a ubiquitous distribution without exceeding the analytical procedure's rejection criterion applied to *Ceratoscopelus warmingi*, *Vinciguerria nimbaria* and the other seven excluded taxa. Group 3 comprised four species of mixed affinities (two island, one oceanic and one other) found in the upper two strata. Although the assemblage occurred most frequently in island waters, total densities were not higher there. Group 4 taxa were

all oceanic but restricted mainly to the upper stratum, whereas group 5 comprised two island taxa restricted mainly to island waters in the upper 100 m. Rarer island taxa characterized group 6, including the carangid *Selar crumenophthalmus* and the apogonid *Apogonichthys perdix*. The last three groups, all oceanic taxa, were most abundant in deeper water, and group 8 was distinguished by its more widespread occurrence of taxa.

DISCUSSION

A variety of studies have documented that planktonic communities near oceanic islands differ from those in the open ocean: near islands, primary productivity [the "island mass effect" in DOTY and OGURI (1956)] and chlorophyll content (HEYWOOD *et al.*, 1990) may be greater. Zooplankton species composition and abundance (JONES, 1962; HERNANDEZ-LEON, 1988), larval fish assemblages (LEIS and MILLER, 1976; SMITH *et al.*, 1987; FEDOR-YAKO, 1989; present study) and acoustic scattering as an indicator of biomass (HARGREAVES, 1975) are all characterized by unique features near islands. Most other studies of ichthyoplankton near islands, however, have considered large islands where surveys could not surround the island (LEIS, 1982b), or island groups where the origin of the neritic larvae could not be determined with certainty (WILLIAMS *et al.*, 1984). In our study, certain components of the ichthyoplankton originating from Johnston Island are retained in near-island waters, typically concentrated in the area downstream of the island (Figs 7 and 8; Tables 2 and 3). A variety of mechanisms may be responsible for the observed distributions, but understanding them may require information on both vertical distribution and physical processes (BAKUN, 1988).

Vertical distribution

The general pattern of vertical distribution, with the peak abundance of both island and oceanic larvae in the 50–100 m stratum (Fig. 5; Table 1), was rather surprising. This is typically deeper than suggested in most studies of tropical ichthyoplankton, especially since all samples were taken at night, when many larvae migrate vertically to shallower water (AHLSTROM, 1959; GORBUNOVA, 1977). We undersampled the neuston, however, and larvae of some taxa probably were more abundant in surface waters than our results indicated.

Patterns of vertical distribution of oceanic fishes in our study were similar to those observed in other studies in tropical and subtropical waters (GORBUNOVA, 1977; LOEB, 1979; CASTONGUAY and MCCLEAVE, 1987). Although the centers of vertical distribution for many of the midwater species are deeper than the sampling in our study (JOHN, 1984), high densities were observed in the strata sampled (Fig. 5; Table 1). Many of the oceanic species we captured were also sampled by LOEB (1979), but her sampling location was farther north, at 28°N. Comparisons of species occurring abundantly in both studies (myctophids *Hygophum proximum* and *Ceratoscopelus warmingi* and the photichthyid *Vinciguerria nimbaria*) demonstrate that the centers of vertical distributions in our study are consistently deeper by 25–75 m. This may be due to temperature; her study site was characterized by a shallow thermocline near 40 m, as opposed to 60–105 m in our study (Fig. 2). Peak larval densities from LOEB (1979) were in the depth stratum containing the thermocline, as was also true in our samples (Table 1). Similarly, night-time distributions of microplankton, mesozooplankton and copepod densities at two stations in the tropics were highest at

"upper thermocline" depths (SAMEOTO, 1986). Thus, temperature in general and the thermocline in particular conceivably play important roles in modifying the vertical distribution of these species. The closer correspondence of our results with thermal profiles and distributions (myctophids *Symbolophorus evermanni*, *Hygophum proximum* and *H. reinhardtii*; photichthyid *Vinciguerria nimbaria*) from equatorial Pacific samples (GORBUNOVA, 1977) supports this interpretation.

Patterns of vertical distribution in tropical island fish larvae have not been described in detail. Most studies describing vertical distribution have been in relatively shallow waters of embayments (WATSON, 1974) or to depths of 6 m in the lagoon of the Great Barrier Reef (LEIS, 1986). MILLER (1979) classified larval vertical distribution patterns as only "surface" or "subsurface". None of these studies is therefore directly comparable with our results, particularly given that the peak abundance of island larvae occurred in the 50–100 m stratum (Fig. 5). Exceptions to this generality include the holocentrids, chaetodontids and *Aulostomus chinensis* in the 0–50 m stratum and the chlopsids, callionymids and *Apogonichthys perdx* in the 100–200 m stratum (Table 1). Some relatively abundant taxa were equally abundant in all strata; the best example is the creediid *Limnichthys donaldsoni*.

Patterns of ontogenetic change in vertical distribution have been noted in several studies (LOEB, 1979; CASTONGUAY and McCLEAVE, 1987); the most common pattern is younger stage larvae at greater abundance in shallower water, moving deeper with increasing length. The opposite was true for certain mid-water taxa, notably *Serrivomer* sp. and *Symbolophorus evermanni* (Fig. 6A). SCHOTH and TESCH (1984) noted that smaller larvae of *Serrivomer beani* in the Sargasso Sea were typically restricted to shallower water. Larvae in our study were not measured and were instead classified as described earlier, so our youngest may be recently hatched larvae. GJOSAETER and TILSETH (1988) suggest that buoyant eggs of *Benthosema pterotum* are spawned deep and that larvae hatch there, moving to shallower habitat with growth; a similar pattern has been noted for *Maurolicus muelleri* (JOHN and KLOPPMANN, 1989). The earliest larvae (<5 mm) of *Anguilla* sp. are relatively deep-living, apparently characteristic of the adult spawning habitat, but later larvae show a pattern of increasing length with depth during the day but not at night (CASTONGUAY and McCLEAVE, 1987). Thus, most of the smallest larvae of *Serrivomer* and *Symbolophorus evermanni* may be present at 100–200 m because of spawning, but the scarcity of yolk-sac larvae precludes confirmation of this pattern. The pattern evident in island fish larvae (that is, younger stage larvae in shallower water; Fig. 6B) also may be related to the shallower spawning habitat.

Horizontal distribution

Several studies of tropical island ichthyoplankton have documented onshore–offshore gradients in abundance (LEIS and MILLER, 1976; LEIS, 1982b). A variety of mechanisms may maintain these gradients. LEIS (1982b) has suggested that larvae distributed offshore are passively advected, whereas those remaining near-shore are characterized by active swimming and the use of favorable currents. Various larval behaviors have been proposed to interact with patterns of upwelling, localized eddies or onshore water movements at various depths to retain the larvae nearshore. Epibenthic schooling (LEIS *et al.*, 1989) or other behavioral mechanisms may allow retention of larvae in shallow water, often directly adjacent to reefs, where they are undersampled in larger scale surveys such as ours (KOBAYASHI, 1989).

On a larger horizontal scale, however, the role of mesoscale oceanographic features in larval distributions must be considered. LOBEL and ROBINSON (1986) proposed that eddies downstream of the Island of Hawaii could both entrain island larvae and later return them to near-shore regions to promote recruitment, but their biological sampling and taxonomic resolution of larvae were inadequate to support this contention. Other studies have documented offshore displacement of spawning and larval habitats for fishes by eddies (FIEDLER, 1986). Topographically controlled fronts around small islands have been shown to accumulate buoyant coral eggs (SAMMARCO and ANDREWS, 1989; WOLANSKI *et al.*, 1989), and creediid eggs have been used as passive tracers of water masses by LEIS (1982a). At Johnston Island, fish eggs were significantly more abundant in the putative downstream retention area in the 50–100 m stratum (Fig. 8), and the larvae of the creediid *Limnichthys donaldsoni* were significantly more abundant in both the 0–50 and 50–100 m strata (Table 2). There may thus be a passive component to the aggregation of fish eggs in the downstream retention area that is maintained by larval behavior after hatching.

HAMNER and HAURI (1981) and WOLANSKI and HAMNER (1988) have described mechanisms by which topographically-induced fronts can result in aggregation of planktonic organisms. The wakes of islands can develop contra-rotating eddies, and BARKLEY (1972) has observed von Kármán vortex streets extending downstream in the wake of Johnston Island. Our objective analysis modeling (Fig. 3) suggests the presence of the margins of two eddies (or meanders) within the domain examined, leading to an area of stagnant waters or possibly return flow that coincided with areas abundant in fish eggs and island larvae. It should be pointed out, however, that the distance of these nominal eddies from Johnston Atoll suggests that they are not produced by currents interacting with the island. Nonetheless, we propose that the situation of return flow leads to the retention of locally spawned eggs and larvae in the vicinity of Johnston Atoll. That the concentrating mechanism does not affect most oceanic species suggests that either larval behavior or localized spawning is required. Both processes may occur for the oceanic scombrid *Thunnus* spp., which may preferentially spawn in waters near islands (MILLER, 1979; LEIS *et al.*, 1991). This is consistent with the trend toward higher abundance of larvae of this genus in the shallow stratum of the downstream retention area (Table 2). For reef fish larvae, however, LEIS (1982b) rejected the hypothesis that higher densities near-shore were the result of a fixed site for spawning followed by dilution and passive drift, again supporting the role of larval behavior.

Without concurrent studies of the spatial and temporal pattern of settlement on the reefs, the importance of our observations to recruitment at Johnston Atoll is uncertain. High densities in the retention area occur at distances far from shore, beyond the swimming capacity of most larvae (Fig. 8), so some form of modulated transport may be necessary to bring larvae competent to settle to nearshore areas. If this is indeed the case, one would expect to see regional variation in the densities of new recruits in reef habitats at the downstream side of the island. Coral recruitment, for example, is highest where flushing rate is low and residence time is high (SAMMARCO and ANDREWS, 1989). Similarly, regional variation in recruitment may be caused by persistent oceanographic features associated with coastal headlands (EBERT and RUSSELL, 1988).

The temporal stability of our putative retention area is also unknown; our sampling occurred over a period of less than 2 weeks. BARKLEY (1972), who described seasonal differences in the incident ocean current patterns at Johnston Island, observed relatively fast (60 cm s^{-1}) incident flow during winter that resulted in a von Kármán vortex street,

but in autumn he observed $15\text{--}20\text{ cm s}^{-1}$ incident flow with no evident wake. The currents observed during the latter period [fig. 2 in BARKLEY (1972)] are remarkably similar to those inferred from dynamic heights in our study during November (Fig. 3). BARKLEY (1972) interpreted the eddies around Johnston Island as part of a line of vortices associated with the frontal zone. However, the slow incident flow evident in summer and autumn may promote the kind of eddies or meanders observed in our study and, concomitantly, the retention of fish larvae in downstream waters. If this feature is seasonally consistent, it would be interesting to determine the spawning seasonality and recruitment patterns of island fish to evaluate the hypothesis that spawning in tropical islands occurs in seasons optimal for retention in island water (JOHANNES, 1978). Existing evidence for this hypothesis is not compelling; ROBERTSON (1990) failed to find a linkage between the seasons of peak spawning and peak recruitment in several species of tropical reef fishes. For Johnston Atoll, the fish fauna is relatively depauperate but is most closely associated with that from Hawaii (RANDALL *et al.*, 1985), where late autumn is the low point in the annual cycle of fish recruitment (WALSH, 1987). Despite our sampling in this season, many species of island larvae were present in moderate to high densities. If the retention area is important for recruitment but temporally infrequent, this would indicate that longer term patterns of recruitment may be driven by more anomalous events (COWEN, 1985; CHOAT *et al.*, 1988; COLIN and CLAVIO, 1988).

Evaluation of these ideas will require further research. Biological studies must determine the ontogenetic changes in vertical and horizontal distributions of larvae, the relative mortality rates of larvae inside retention areas and the resulting patterns of recruitment to the island. A better understanding of the physical oceanography will be required to assess the persistence of larval retention, with direct measurement of currents and tidal flux relative to larval advection.

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Abstract.—To resolve the uncertainty in estimating capture depths of fish on pelagic longline gear, electronic microchip hook timers were attached to branch lines to record when bites occurred, and time-depth recorders (TDRs) were attached to longline gear, off Hawaii in January 1989 and January–February 1990. Hook timers indicated that 32% of the striped marlin *Tetrapturus audax*, 21% of the spearfish *T. angustirostris*, and 12% of the bigeye tuna *Thunnus obesus* were caught on sinking or rising hooks, demonstrating that capture time data are needed to correctly estimate capture depth. Recorded and predicted longline depths differed greatly, indicating that TDRs are essential for describing depth distributions of fish from longline catches. Most (>60%) of the spearfish and striped marlin were caught on settled hooks (not sinking or rising) at depths of <120 m, whereas most bigeye tuna were caught at depths of >200 m. This suggests that eliminating shallow hooks could substantially reduce the bycatch of spearfish, striped marlin, and other recreationally important billfish without reducing fishing efficiency for bigeye tuna. Bigeye tuna and striped marlin survived up to 6–9 hours after capture, and over 50% of 12 frequently-caught taxa were alive when retrieved, suggesting that the release of live fish can be an effective management option.

Depth, capture time, and hooked longevity of longline-caught pelagic fish: Timing bites of fish with chips

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Targeting specific depths can improve longline catches of desired species, such as bigeye tuna *Thunnus obesus* (Saito 1975, Hanamoto 1976, Suzuki et al. 1977, Suzuki and Kume 1982), and reduce bycatch of other species, such as billfish (Suzuki 1989). However, considerable uncertainty exists in estimating the fishing depth of longline gear. Predicted longline depth based on catenary geometry, line length, and distance between floats (Yoshihara 1954) differs from true depth (Saito 1973, Hanamoto 1974, Nishi 1990) because of currents and other factors, yet depth is often inferred rather than measured (Suzuki et al. 1977, Suzuki and Kume 1982, Hanamoto 1987, Grudinin 1989). Furthermore, fish may be caught while the hooks are sinking, during deployment of the gear, or rising during its retrieval (Saito 1973), making capture depths impossible to estimate accurately without known capture times.

Accurate estimates of fishing depth can be made if time-depth recorders (TDRs) are attached to longline gear. Longline studies using TDRs (Saito et al. 1970, Saito 1973, Yamaguchi 1989, Nishi 1990) have also interpreted TDR depth fluctuations as records of times of capture, but few such measurements exist. Instead, capture has been assumed to occur when the gear is settled, so capture depth has been estimated as settled hook depth (Hanamoto 1976, Suzuki and Kume 1982). Hook timers, de-

signed to indicate when each hook is struck (Somerton et al. 1988), provide a way to measure capture times and survival times of hooked fish. Capture times, together with TDR records, can be used to estimate capture depths accurately.

Billfish catch rates in recreational fisheries may be negatively affected by nearby longline fisheries (Squire and Au 1990), and interest in finding ways to reduce the longline take of billfish without reducing fishing efficiency for target species is increasing (Rockefeller 1989). Information on capture depth, capture time, and hooked longevity can be used to design fishing methods that reduce billfish mortality. Data on the selectivity and efficiency of longline gear at various depths are also critical for stock assessments (Suzuki 1989).

The present study improves methods for estimating capture depths of fish on longline gear using electronic timing devices, and describes the depth distributions and capture times of tunas, billfishes, sharks, and other pelagic fishes in Hawaiian waters in winter. Water temperature and dissolved oxygen (DO) were measured to describe the physical habitat in the study area, since these variables appear to cause geographic variation in depth distributions of fish (Hanamoto 1975, 1987). Relative fishing efficiency and the bycatch of billfish were predicted for several gear configurations.

Table 1

Summary of longline fishing operations conducted by the NOAA ship *Townsend Cromwell* off Hawaii, January 1989 and January–February 1990, giving averages for three set types (ranges in parentheses). Baskets were intervals of continuous main line between floats with snap-on branch lines, not spliced units of gear. Shortening rate was the ratio between ship speed and thrower speed. Depths do not include branch line length. Predicted depths were calculated from the shortening rate and the main line length per basket, assuming a catenary shape. TDR = time depth recorder.

Year	Set type	Sets (no.)	Time		Hooks per set (no.)	Line per basket (m)	Shortening rate (ratio)	Predicted depth (m)	Deep TDR depth (m)	Middle TDR depth (m)
			Begin set	End retrieval						
1989	Regular	6	8:09	15:24	199	795	0.80	222	111 ¹	82 ²
			(4:31–10:05)	(14:20–16:41)	(128–278)	(640–1103)	(0.69–0.98)	(88–304)	(43–180)	(32–133)
	Deep	6	8:55	16:36	257	1085	0.59	415	260	191 ²
			(5:29–12:47)	(10:34–20:40)	(185–392)	(990–1146)	(0.46–0.83)	(273–489)	(241–303)	(178–224)
	Very deep	4	8:23	19:10	405	1117	0.54	447	367	270 ²
			(8:16–8:41)	(17:58–20:40)	(356–474)	(1053–1146)	(0.45–0.71)	(349–496)	(329–400)	(243–295)
1990	Regular	5	6:50	19:08	456	809	0.78	243	142	104
			(6:14–7:18)	(16:24–22:07)	(212–591)	(611–1068)	(0.67–0.90)	(150–355)	(78–183)	(71–140)
	Deep	13	7:18	19:38	474	1069	0.60	409	249	180
			(6:12–10:04)	(17:57–20:42)	(173–594)	(798–1265)	(0.40–0.70)	(298–499)	(193–318)	(122–232)
	Very deep	4	5:29	19:03	404	1165	0.62	436	416	291
			(4:45–6:21)	(15:30–21:05)	(219–600)	(937–1427)	(0.50–0.74)	(303–592)	(340–517)	(251–381)

¹TDR data obtained for only three sets.

²Calculated from the ratio (0.73) between middle and deep TDR depths of sets in which middle-position data were available.

Materials and methods

Longline fishing was conducted on board the NOAA ship *Townsend Cromwell* in January 1989 and January–February 1990. Sets were made between lat. 14° and 20°N, long. 148° and 159°W, 20–500 nmi from the main Hawaiian Islands, and within an area typically fished by Hawaii's domestic longline fishery. Gear was usually deployed in the morning and retrieved in the afternoon or evening (Table 1), or occasionally at mid-day to permit a second set on the same day. No sets were made at night. Except for the hook timers and TDRs, the fishing gear and operations were similar to commercial longline fishing methods for tuna in Hawaii (Kawamoto et al. 1989) prior to the advent of night fishing for swordfish *Xiphias gladius*. Both this study and the contemporary commercial longline fishery used a wide variety of fishing depths. Commercial fishermen used more gear (~1000 hooks), let it stay in the water longer (~12h), and retrieved it faster than in this study.

The fishing gear consisted of 3.5 mm-diameter nylon monofilament main line deployed with a line thrower (Kawamoto et al. 1989). The main line was supported at intervals by vertical, 18 m lines with floats at the ends. Snap-on branch lines made of 2.1 mm-diameter clear-blue nylon monofilament (20 m long in 1989 and 11 m long in 1990) were baited with thawed saury *Colo-labis saira* on curved tuna hooks (one hook/branch line) and attached to the main line between float lines.

Hooks were size 3.6 (Japanese size is 10.9 cm from eye to point). Each portion of the longline between floats and the attached branch lines constituted a "basket," a term taken from older gear in which the number of branch lines is fixed. However, this study used varying numbers of snap-on branch lines (12, 14, 16, or 20/basket), depending on the length of main line per basket.

Hook position was controlled by timing the attachment of branch lines as the main line was thrown overboard mechanically at a controlled speed. A computer program was used to signal and record attachment times. Deviations from the programmed instructions were noted, providing a record of set times for each hook. The total number of hooks in each set was 128–600, and the amount of main line deployed per set was 9–44 km (Table 1). The amount of gear increased with crew experience but also varied because of inclement weather and equipment failures.

Set depths

Fishing depth was altered by varying the slack in the main line and the length of line per basket (Table 1) and by exogenous factors such as wind and currents. Line slack was quantified as the shortening rate (Saito 1973), or sagging rate (Suzuki et al. 1977), equal to the horizontal distance between floats divided by the length of line per basket (a dimensionless ratio). At deploy-

ment, the shortening rate was the same as the ratio of ship speed through the water to line-thrower speed: 0.40 (maximum slack) to 0.98 (no slack). The length of main line per basket was 640–1427 m. The predicted maximum depth of the main line during each set was calculated from the shortening rate and the main line length per basket (Table 1), assuming a catenary shape (Yoshihara 1954).

The depth of each set was recorded with electronic TDRs (Wildlife Computers, models MKII and MKIII) programmed to sample depth once per minute. The TDRs were attached at the deep positions, defined as the attachment points for the branch line midway between floats (e.g., position 10 or 11 of 20 between floats). In 1990, TDRs were also attached at the middle positions between the deep positions and the float line (e.g., at position 5 or 15 of 20 between floats).

The time that the gear took to sink during deployment (0.5 h) and to rise during recovery (0.5 h) was quantified from TDR records. Set depth was described as the typical depth observed in records from the deep-positioned TDRs during the period after sinking and before rising. Recorded depth was examined after each set and compared with predicted depth. Shortening rate, the length of line per basket, or both were adjusted in the subsequent set to reach targeted depths.

Hook depths

The settled depth of each attachment point for the branch line was estimated by interpolating between (1) the TDR record for the deep and middle positions or (2) the latter point and the shallowest depth of the main line (assumed to equal the length of the float line). Settled hook depth was calculated by adding the branch line length to the interpolated depth of the branch line snap. Not enough TDRs were available (2 in 1989, 10 in 1990) to put 1 TDR on every basket. When fish were caught by baskets without TDRs, average TDR depths for that set were used to interpolate settled hook depths. For middle positions without TDRs in 1989, depth was estimated from the mean ratio of the middle position to deep-position TDR depths based on 1990 data.

Hook timers

Hook timers were made of a plastic resin cast around a battery-powered microchip clock controlled by a magnet (Somerton et al. 1988). They were attached to the branch lines near the snap, bridging a bend in the line (Fig. 1). A fish striking the hook pulled the magnet, thus triggering the timer. In 1989, a rubber band held the magnet in place against a test weight of about 1–2 kg. In 1990, thread with a breaking strength of

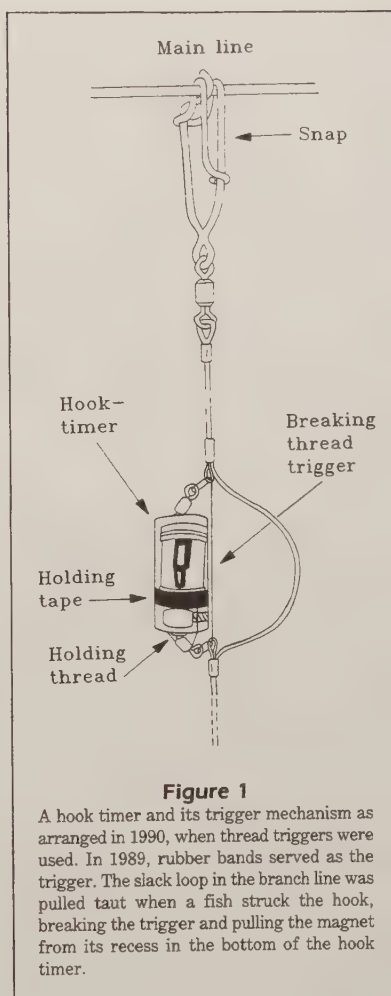


Figure 1

A hook timer and its trigger mechanism as arranged in 1990, when thread triggers were used. In 1989, rubber bands served as the trigger. The slack loop in the branch line was pulled taut when a fish struck the hook, breaking the trigger and pulling the magnet from its recess in the bottom of the hook timer.

4–5 kg bridged the bend in the line, and the magnet was held in place by a weaker thread until the bridging thread was broken (Fig. 1). Some branch lines were set without timers (14% in 1989, 35.5% in 1990) to preclude interruptions in fishing when timers were tangled or otherwise unavailable.

Hook timers indicated elapsed time in whole minutes (e.g., 0 min indicated 0–59 s). Timers were read as the branch lines were recovered, or soon after, with corrections made for delays. Timers were categorized as being triggered (1) at recovery (≤ 1 min before removing the branch line snap), (2) while rising (> 1 min–0.5 h before recovery), (3) while settled (> 0.5 – < 1.0 h, 1 – < 2 , 2 – < 3 h, and so on before recovery), (4) while

sinking (<0.5 h after gear deployment), (5) at deployment (≤ 2 min after deployment), and (6) before deployment (timer triggered before setting commenced). Timers activated but without fish were categorized similarly except all settled categories (>0.5 – 9.0 h) were combined. Untriggered hook timers with fish also were tallied, and hooks with timers that were damaged, broken loose, or tangled too badly to be triggered were counted as hooks without timers.

The numbers of fish caught while the gear was sinking, settled, and rising were summarized. The unconfirmed depth of capture of each fish was defined as the settled depth of the hook. Capture depths were considered confirmed only if hook timers indicated the capture occurred within the period in which the gear was settled.

Catch and effort

Live fish that were not needed as specimens were tagged and released. Steel head "H" type dart tags (Squire 1987) were applied using a 3m tagging pole while the fish remained in the water. Billfish were also injected with 5–20mg oxytetracycline/kg of fish using pole-mounted syringes (Foreman 1987) to mark hard parts for validation of growth increments. Fish were released by cutting the branch lines close to the hooks with a tree-trimming pole. The condition (alive or dead) of the retained fish was noted, and it was weighed to the nearest 0.5kg or measured to the nearest 0.1cm. For the five most-frequently-caught species of commercial importance, catch, number of hooks, and number of hooks with timers were stratified into 40m strata (40 – <80 m, 80 – <120 m, and so on) based on settled hook depths. The catch-per-unit-effort (CPUE) in each depth stratum was examined in two ways: (1) by confirmed capture depth ($CPUE_D$ in number of fish/1000 hooks with timers) representing the depth distribution of fish; and (2) by settled hook depth ($CPUE_H$ in number of fish/1000 hooks), representing the total effectiveness of hooks while sinking, settled, or rising.

The $CPUE_H$ for each depth was used to predict catch rates of "standardized" types of gear to illustrate the use of catch by hook position in estimating relative gear efficiency for different gear configurations. Total CPUE for each standardized gear configuration was estimated by calculating the weighted average $CPUE_H$, with weights corresponding to a given number of hooks per depth stratum for each configuration. Total CPUE was calculated from 1989 and 1990 data separately and averaged. Gear efficiency was calculated as the ratio of the predicted CPUE for each configuration to that of the regular configuration.

Standardized regular and deep longline gear configurations were assumed to have 6 and 13 hooks/basket,

respectively. A shortening rate of 0.6 and the dimensions in Suzuki et al. (1977; without adjustment for currents) indicated hook depths of about 95, 140, and 170m (for regular gear) and 100, 145, 190, 230, 265, 290, and 300m (for deep gear). These depths correspond roughly to the midpoints of hook depth strata in the present study (100, 140, 180, 220, 260, and 300m).

In addition to regular and deep gear, CPUE values for two hypothetical gear types were predicted: (1) shallow gear for which hooks are limited to the first three depth strata of this study; and (2) a proposed new gear for which no hooks would be deployed in the first three depth strata and the distribution of deeper hooks would match that of deep gear. The shallow gear configuration may be representative of that achieved by Hawaii's longline fishermen in 1989 and 1990 when they first began using monofilament longline and had difficulty achieving the depths formerly fished with traditional rope gear. With the rope gear, slack was obtained by manually throwing the baskets with the main line partially coiled. The [predicted] CPUE for the new gear type was estimated to indicate the reduction in bycatch of some species by the elimination of shallow hooks.

To show CPUE as it would appear in a study of gear configurations without hook position, capture depth, or capture time information, $CPUE_S$ values were calculated from catch and effort by set type. Sets were categorized on the basis of depth (TDR depth plus branch line length) into three groups: 60– <200 m (regular), 200– <330 m (deep), and 330–530m (very deep). The first two groups contained depth ranges roughly comparable to those expected for regular and deep longline gear types, assuming a variety of shortening rates and variation due to ocean currents (Suzuki et al. 1977).

Oceanography

Vertical temperature structure in the area of each set was measured by expendable bathythermographs (XBTs; 400m depth) and conductivity-temperature-depth casts (CTDs; 500–1000m depth, usually 500m) before or after each set. Water samples were taken with Niskin bottles to measure DO and to calibrate DO measurements made by CTDs.

Many of the TDRs were equipped with a second channel to record temperature. The TDRs were attached to the CTD probe to calibrate depth and temperature measurements. The TDR temperature data were used to estimate set depths exceeding 400m (the lower limit for accurate range depth measurement from the TDRs).

Table 2

Catch data for 14 frequently-caught taxa in research longline sets off Hawaii, January 1989 and January–February 1990. Some weights were calculated from length measurements; some fish (i.e., those released) were not weighed.

Species	No. caught	No. weighed or measured	Weight (kg)		Alive (%)
			Average	Range	
Bigeye tuna <i>Thunnus obesus</i>	76	32	31.5	2.5–69.5	83
Yellowfin tuna <i>T. albacares</i>	16	11	39.5	7.5–62.5	63
Skipjack tuna <i>Katsuwonus pelamis</i>	5	5	9.0	7.0–11.0	20
Wahoo <i>Acanthocybium solandri</i>	4	3	17.5	7.5–25.0	0
Striped marlin <i>Tetrapturus audax</i>	67	20	18.0	9.5–37.0	71
Spearfish <i>T. angustirostris</i>	41	23	13.5	8.5–18.5	56
Mahimahi <i>Coryphaena hippurus</i>	90	60	6.5	2.5–16.0	88
Pomfrets (Bramidae)	17	15	5.5	2.0–10.0	86
Lancetfish <i>Alepisaurus ferox</i>	132	111	1.5	0.1–8.0	64
Ribbonfish <i>Trachipterus ishikawae</i>	4	2	8.0	7.0–8.0	75
Brown ray <i>Dasyatis violacea</i>	8	4	2.0	1.0–2.5	88
Whitetip shark <i>Carcharhinus longimanus</i>	26	—	—	—	85
Blue shark <i>Prionace glauca</i>	21	1	68.0	—	100
Thresher shark <i>Alopias</i> spp.	6	1	91.0	—	60

Results

A total of 16 longline sets caught 149 fish in 1989 and 22 sets caught 401 fish in 1990. Fishing effort totaled 14,410 hooks including 10,236 hooks with timers. There were 14 taxa for which more than 3 fish were caught (Table 2).

Achieving deep sets when intended was sometimes difficult. Backlash of the main line into the hydraulic line thrower created problems at high thrower speeds, and ship speed through the water was sometimes underestimated, reducing the shortening rate. Wind and currents reduced set depth by dragging floats and parts of the line in opposing directions. In particular, current shear between the surface and the waters below the thermocline, observed with an acoustic Doppler current profiler, seemed to prevent deep sets. Observed set depths were highly variable and usually less than the predicted depths (Table 1, Fig. 2). For example, at a predicted depth of about 490m, observed depths were 200–400m (Fig. 2). Sets averaged only 54% and 68% of the predicted depths in 1989 and 1990, respectively. For the first three sets in 1989, the TDRs failed, so depth was estimated as a percentage of the predicted depth based on the average percentage (49.3%) obtained from the next three sets with similar configurations.

Capture depths

Capture depths were confirmed for those fish caught >0.5h after deployment and >0.5h before retrieval,

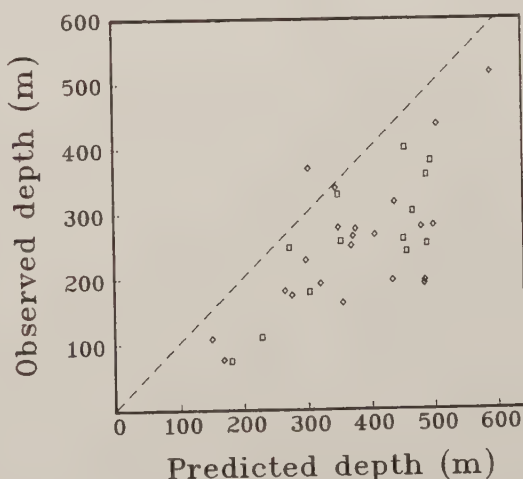


Figure 2

Relationship between predicted and observed set depths in 1989 (□) and 1990 (◇). Observed depths were measured with time-depth recorders, and predicted depths were calculated from the shortening rate and the main-line length per basket, assuming a catenary shape.

because the TDR records showed that the main line usually took 0.5h to sink to within about 90% of its settled depth and about 0.5h to rise to the surface during retrieval (Fig. 3). Records of settled depth sometimes varied ≤ 100 m for the deep sets (e.g., set 14;

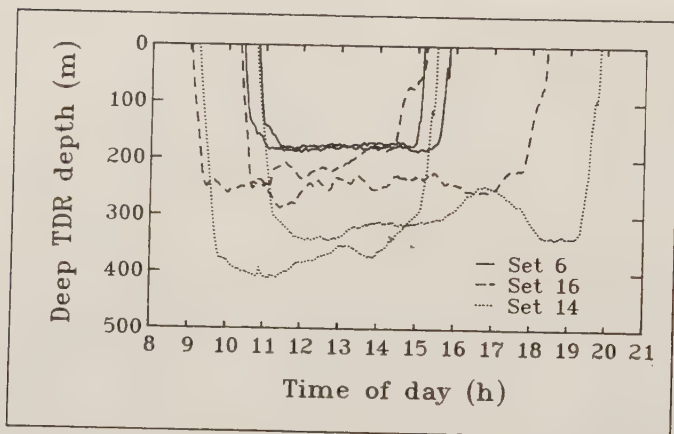


Figure 3 (left)

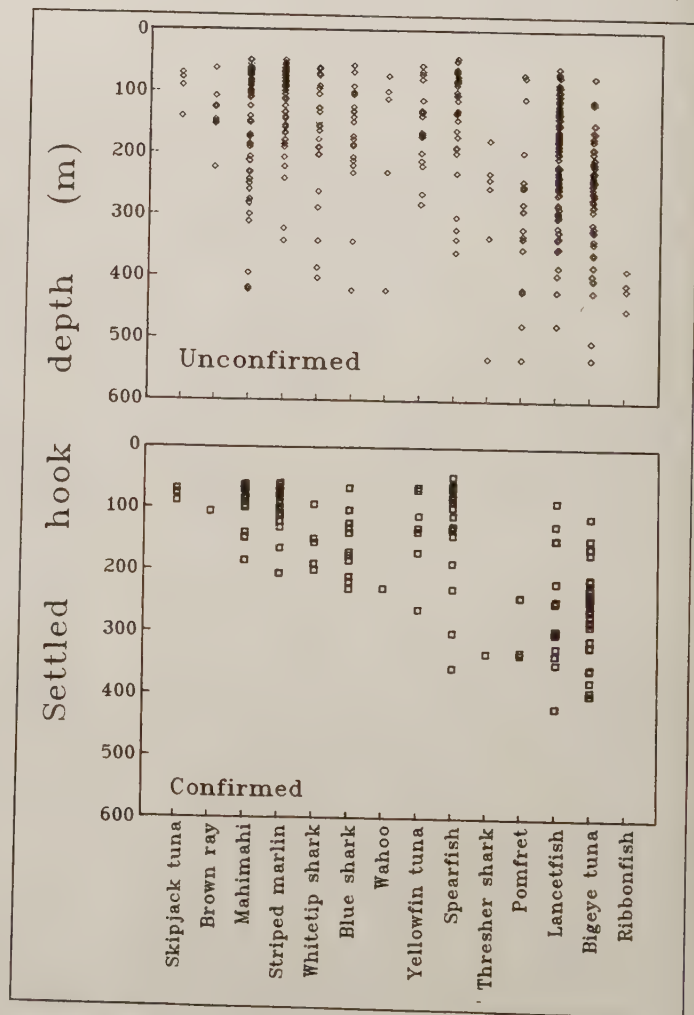
Sample records from time-depth recorders (TDRs) measuring the deep positions on three sets (each with two TDRs) in 1989, illustrating the typical sinking time (0.5h), variation in settled depth, and typical rising time (0.5h).

Fig. 3) and ≤ 40 m for the regular sets. Also, the gear sometimes took more than 0.5 h to rise (e.g., the first TDR on set 16; Fig. 3) or sink. Such deviations contributed to the variation in estimated capture depths. Capture depths of fish caught with hook timers on baskets with TDRs were based on the TDR depth at the time of capture; however, most catches were made by baskets without TDRs.

A comparison between the unconfirmed depths of all hooks that caught fish and those confirmed to have caught fish while settled (Fig. 4) showed that without hook-timer confirmation, many fish appeared to be caught at greater depths than they actually were. For example, mahimahi *Coryphaena hippurus* had unconfirmed capture depths of ≤ 420 m and confirmed capture depths of < 190 m. Most confirmed capture depths were < 100 m for mahimahi and skipjack tuna *Katsuwonus pelamis*. Striped marlin *Tetrapturus audax*, whitetip shark *Carcharhinus longimanus*, blue shark *Prionace glauca*, and wahoo *Acanthocybium solandri* had unconfirmed depths of ≤ 350 – 420 m and confirmed depths of < 200 – 230 m. Species having a preponderance of confirmed capture depths of < 150 m were yellowfin tuna *Thunnus albacares*, striped marlin, and spearfish *Tetrapturus angustirostris*. Most confirmed capture depths were > 200 m for thresher

Figure 4 (below)

Hook depths for catches of 14 frequently-caught taxa in a study off Hawaii, winter 1989 and 1990 (combined). Settled hook depths are shown for all hooks that caught fish (unconfirmed) and for those hooks that caught fish while settled (i.e., not sinking or rising) as indicated by hook-timer data (confirmed).



shark *Alopias* spp., pomfrets (Bramidae; species included *Taractichthys steindachneri*, *Taractes rubescens*, and *Eumegistus illustris*), lancetfish *Alepisaurus ferox*, and bigeye tuna (Fig. 4).

Capture times

Most of the fish (except ribbonfish *Trachipterus ishi-kawae* and brown ray *Dasyatis violacea*) were caught

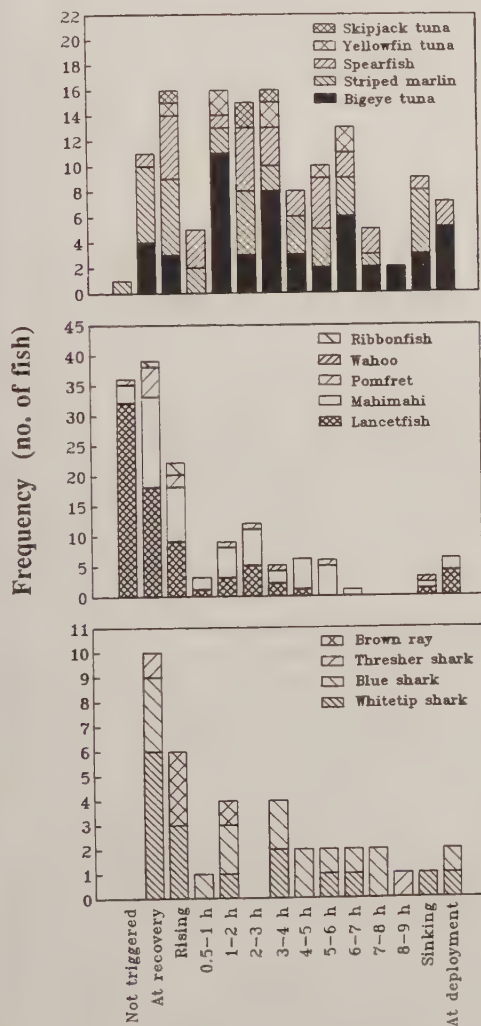


Figure 5

Hook-timer data for 14 taxa caught off Hawaii, winter 1989 and 1990 (combined). Height of each bar represents the sum of frequencies for each taxa (stacked bars). Hook timers were either not triggered, triggered while the gear was being set or recovered, or triggered by fish caught while gear was sinking, settled (0.5-9.0 h before recovery), or rising.

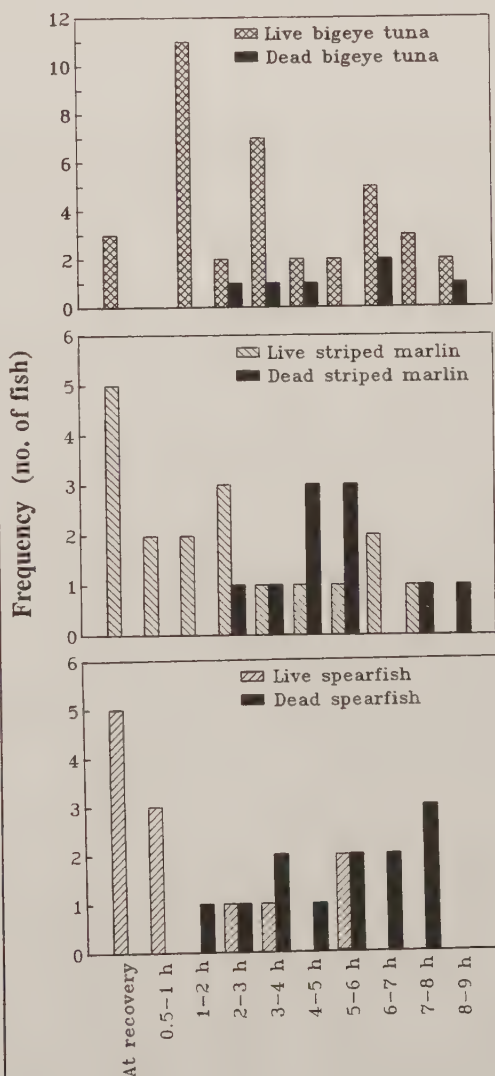


Figure 6

Condition (alive or dead) of three important species in relation to the elapsed time between capture and recovery as indicated by hook timers, during a study off Hawaii, winter 1989 and 1990 (combined).

while the gear was settled rather than while it was sinking or rising (Fig. 5), probably because the gear spent much more time in the settled position. However, substantial numbers of mahimahi, billfish, and other species were caught while the gear was rising (Fig. 5), which explains how fish were caught on deep-positioned hooks (unconfirmed depths) when their confirmed depth distribution was shallow (confirmed depths; Fig. 4).

For many species, catch-per-unit-time (CPUT) may have been highest while the gear was rising. The CPUT values at <3 and ≥ 3 h before recovery were not directly comparable because short sets resulted in lower effort (number of hooks with timers) ≥ 3 h before recovery. The catch in the 1–2 h and 2–3 h periods (Fig. 5) must be divided by 2 for comparison with the CPUT in the 0.5 h and 0.5– <1.0 h periods. For periods of 0.5–1.0, 1–2, and 2–3 h before recovery, CPUT values were less than during the rising period for ribbonfish, pomfrets, mahimahi, lancetfish, striped marlin, spearfish, brown ray, and whitetip shark (Fig. 5). In contrast, the values for yellowfin and skipjack tunas were not much different between settled and moving gear and were highest for bigeye tuna 1–2 h and 3–4 h before recovery. Blue shark CPUT values were highest 1–2 h before recovery.

Relatively large numbers of fish were categorized as caught at recovery (Fig. 5). However, estimates of the delay between recovery and reading each timer were not precise (± 1 minute). Thus some fish caught "at recovery" actually had timers triggered after recovery. Hook timers that did not catch fish were most often triggered "at recovery" (Table 3), suggesting that handling activated the timers. A similar lack of precision affected capture times "at deployment."

Hooks with timers triggered by small fish or without catching fish may have resulted in false capture times if larger fish were caught later on those hooks. Fortunately, small (<10 kg) fish, particularly lancetfish (Table 2), were most frequently caught without triggering the timers (Fig. 5). It was unusual for larger (~ 10 – 90 kg) fish, such as tunas, billfishes, or sharks (Table 2, Fig. 5), to be caught without triggering the timers. The increase in breaking strength of the triggers in 1990 (Fig. 1) decreased the relative number of small fish that triggered timers, and reduced the proportion of timers triggered without catching fish from 18.5% in 1989 to 9.7% in 1990 (Table 3).

Survival and release

Over 56% of the fish other than wahoo and skipjack tuna were alive when recovered, and for most species, survival was higher than 70% (Table 2). Based on fish with hook-timer data, over half of the bigeye tuna recovered up to 9 h after capture were alive. None of the 11 bigeye tuna recovered 1–2 h after capture were dead, and the shortest period between capture and recovery of dead bigeye tuna was 2–3 h (Fig. 6). Striped marlin were less hardy, with over half recovered dead ≥ 3 h after capture; nevertheless, many were recovered alive up to 6–8 h after capture (Fig. 6). Spearfish were the least hardy: The longest survival time was 5–6 h, and dead fish were recovered at <1 –2 h after capture (Fig. 6).

Of the 29 bigeye tuna, 35 striped marlin, and 11 spearfish tagged during the study, 2 bigeye tuna and 1 striped marlin were recaptured 3–10 months later. These three fish were tagged after having been on branch lines for 3–6 h. The marlin had been injected

Table 3

Frequencies of activated hook timers on branch lines without fish (as percentage of total timers) categorized by elapsed time since the timers were triggered (range of values from individual sets in parentheses).

Year	Elapsed time					Activated before deployment	No. timers	Branch lines with timers (%)
	Before retrieval			After deployment				
	At retrieval (≤ 1 min)	Rising (> 1–30 min)	Settled (≥ 30 min)	Sinking (≤ 30 min)	At deployment (≤ 2 min)			
1989	6.4 (—)*	1.2 (0–3.2)	3.9 (0.8–7.1)	1.0 (0–5.7)	4.8 (1.6–7.1)	1.0 (0–3.3)	3744 (126–356)	86.0 (61–100)
1990	3.8 (1.1–6.2)	1.5 (0–4.8)	2.6 (0.8–6.5)	0.4 (0–1.1)	1.0 (0–2.6)	0.4 (0–2.4)	6492 (167–418)	64.5 (34–99)
Combined	4.7*	1.4	3.1	0.6	2.4	0.6	10236	71.0

* Number recorded only during the first set in 1989. To calculate the combined frequency (4.7%), frequency was assumed to be 6.4% throughout 1989.

with 6 mg/kg oxytetracycline, but no fluorescent mark was found in the otolith or vertebrae.

Abundance in relation to depth

For bigeye tuna, the depth distribution of $CPUE_D$ values (number of fish/1000 hooks with timers) was similar in 1989 and 1990, with $CPUE_D$ highest at 360–400 m and relatively high at 200–400 m (Fig. 7). Hooks with timers triggered before or at deployment could not be subsequently triggered; therefore, they were counted as hooks without timers when $CPUE_D$

was calculated (Table 4). The data from wider depth ranges in both years were pooled to obtain sample sizes (number of hooks with timers; Table 4) large enough to determine whether significant differences existed between depths (Fig. 8). For bigeye tuna, $CPUE_D$ values were significantly higher at depths of >200 m than at depths of <200 m ($P < 0.05$, based on 95% CI for the difference between proportions). Few (12%) of

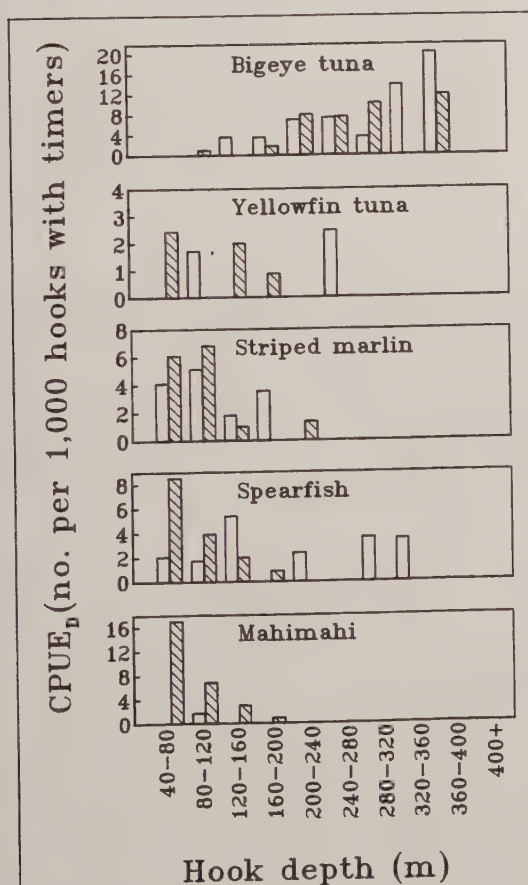


Figure 7

Indices of fish abundance vs. depth, calculated as the number of fish caught/1000 hooks with timers ($CPUE_D$) in ten depth strata. Indices for 1989 (open bars) and 1990 (crosshatched bars) are based on fish captured while the gear was settled (as confirmed by hook timers) (Table 4).

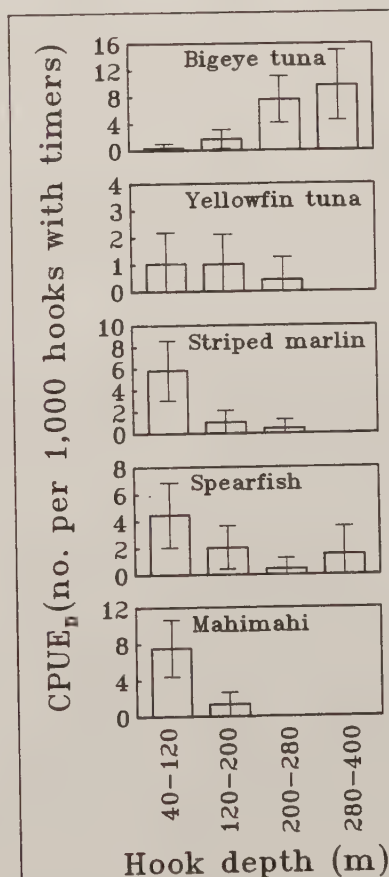


Figure 8

Indices of fish abundance vs. depth, calculated as the number of fish caught/1000 hooks with timers ($CPUE_D$) in four pooled hook-depth strata. Indices for 1989 and 1990 combined are based on fish captured while the gear was settled (as confirmed by hook timers) (Table 4). Error bars indicate 95% CI of the $CPUE_D$ values for each depth category.

the bigeye tuna with hook timers were caught while the hooks were moving (sinking or rising; Table 4). No clear relationship existed between depth and the proportion caught on moving hooks (Table 4).

Yellowfin tuna were not very abundant, which is typical for the winter months off Hawaii. The CPUE_D for yellowfin tuna was not the same in both years (Fig. 7), but the number of fish caught with timers was very small, particularly in 1989 (Table 4). Pooled CPUE_D was highest at 40–200 m (Fig. 8) although no significant difference in CPUE_D by depth was found. The 40 m end of the depth range did not indicate the shallowest depths preferred by any species, since no hooks fished depths of <40 m.

Timer-confirmed catches by settled hooks indicated the highest catch rates for striped marlin were at 40–120 m in both years (Fig. 7), and pooled CPUE_D was clearly the highest at this depth range (Fig. 8). The overall proportion of striped marlin caught on moving hooks was high (32%; Table 4) and increased with

depth. At >120 m most striped marlin were caught by moving hooks, and at >200 m only one was caught by a settled hook (Table 4).

For spearfish, the pattern of CPUE_D vs. depth differed between years. In 1989, the highest CPUE_D was at 120–160 m although several fish were caught as deep as 280–360 m; however, in 1990 the highest CPUE_D was at 40–80 m, and no confirmed capture depths were recorded at >200 m (Fig. 7). Pooled data suggested that spearfish were more abundant at <120 m, but the CPUE_D at 40–120 m was not significantly different from that at 120–200 m (Fig. 8). In 1989, a large proportion (43%) of the spearfish were caught on moving hooks, but none were caught on moving hooks in 1990 (Table 4). Furthermore, for each of the major species, a higher proportion of fish were caught on moving hooks in 1989 than in 1990 (Table 4). An early report (Boggs 1990) on this research was based on 1990 data (Table 4) wherein only 12% of the tuna and billfish (combined) were caught on moving hooks.

Table 4

Catch of five commercially-important species in research longline sets off Hawaii, 1989 and 1990, giving fishing effort (number of hooks and timers) by depth strata, number caught (*N*) on known hook position, number confirmed by timers to be caught on moving (*M*; i.e., sinking or rising) and settled (*S*) hooks (in parentheses), and percentage of fish caught on moving hooks. Depth ranges include branch line length. Timers do not include those triggered at or before deployment. Catch totals are sometimes less than in Table 2 and Figure 5 because hook number and depth were not known for a few fish.

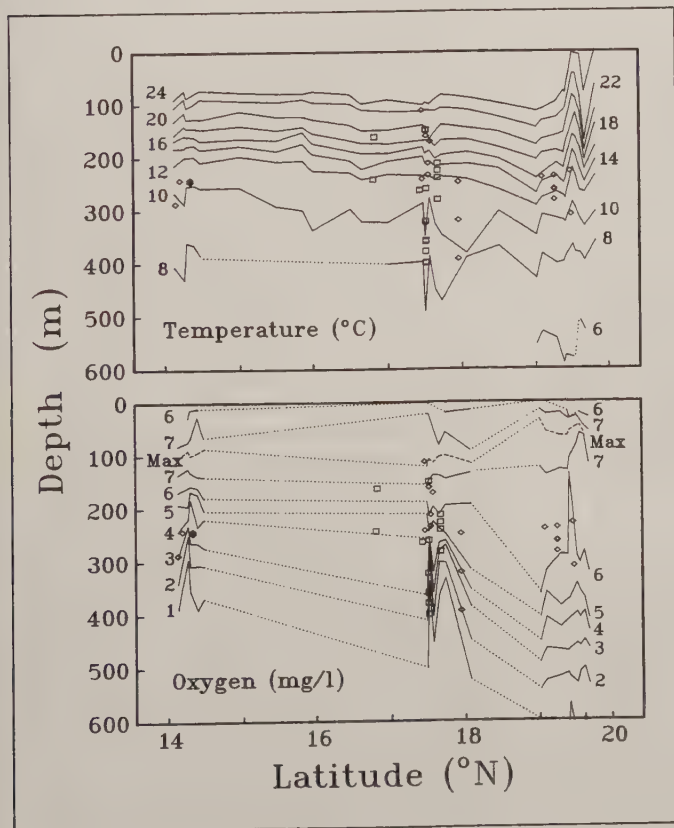
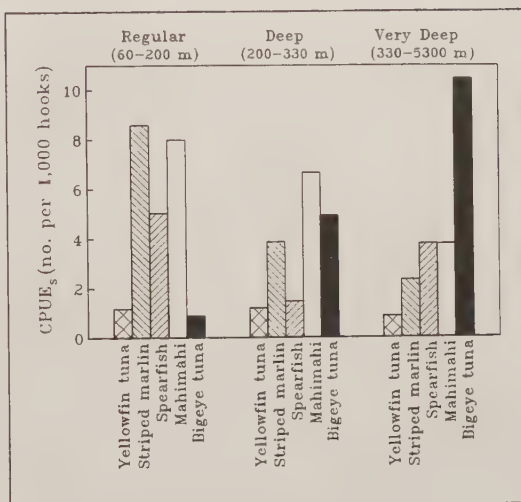
Hook depth (m)	Year	Hooks in stratum	Timers in stratum	Bigeye tuna		Yellowfin tuna		Striped marlin		Spearfish		Mahimahi	
				<i>N</i> (M, S)	Moving (%)	<i>N</i> (M, S)	Moving (%)	<i>N</i> (M, S)	Moving (%)	<i>N</i> (M, S)	Moving (%)	<i>N</i> (M, S)	Moving (%)
40–80	1989	546	489	1 (0, 0)	—	0 (0, 0)	—	5 (0, 2)	0	4 (1, 1)	50	3 (0, 0)	—
	1990	1214	822	0 (0, 0)	—	4 (0, 2)	0	16 (1, 5)	17	8 (0, 7)	0	41 (5, 14)	26
80–120	1989	684	586	0 (0, 0)	—	1 (0, 1)	0	9 (1, 3)	25	4 (1, 1)	50	2 (0, 1)	0
	1990	1612	1026	2 (0, 1)	0	0 (0, 0)	—	15 (2, 7)	22	5 (0, 4)	0	14 (1, 7)	12
120–160	1989	658	558	2 (0, 2)	0	0 (0, 0)	—	6 (2, 1)	25	5 (1, 3)	25	1 (0, 0)	—
	1990	1611	1007	0 (0, 0)	—	3 (0, 2)	0	3 (1, 1)	50	3 (0, 2)	0	5 (1, 3)	25
160–200	1989	350	281	1 (0, 1)	0	0 (0, 0)	—	2 (1, 1)	50	1 (1, 0)	100	0 (0, 0)	—
	1990	1812	1151	6 (1, 2)	33	4 (0, 1)	0	5 (1, 0)	100	5 (0, 1)	0	6 (0, 1)	0
200–240	1989	553	427	6 (1, 3)	25	1 (1, 0)	100	2 (0, 0)	—	1 (0, 1)	0	1 (1, 0)	100
	1990	1160	748	11 (1, 6)	14	1 (0, 0)	—	1 (0, 1)	0	0 (0, 0)	—	4 (0, 0)	—
240–280	1989	524	406	5 (0, 3)	0	1 (0, 1)	0	0 (0, 0)	—	0 (0, 0)	—	1 (0, 0)	—
	1990	1321	795	11 (0, 6)	0	1 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	6 (1, 0)	100
280–320	1989	353	279	3 (0, 1)	0	0 (0, 0)	—	0 (0, 0)	—	1 (0, 1)	0	1 (0, 0)	—
	1990	626	395	7 (0, 4)	0	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	1 (0, 0)	—
320–360	1989	384	288	7 (1, 4)	20	0 (0, 0)	—	2 (1, 0)	100	4 (2, 1)	67	0 (0, 0)	—
	1990	198	152	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—
360–400	1989	214	148	6 (1, 3)	25	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—
	1990	108	84	2 (0, 1)	0	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	1 (0, 0)	—
400+	1989	87	60	2 (0, 0)	0	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—
	1990	276	225	2 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	0 (0, 0)	—	2 (1, 0)	100
Total	1989	4352	3522	33 (3, 17)	15	3 (1, 2)	33	26 (5, 7)	38	20 (6, 8)	43	9 (1, 1)	50
	1990	10,058	6402	41 (2, 20)	9	13 (0, 5)	0	40 (5, 14)	26	21 (0, 14)	0	80 (9, 25)	26
Combined total		14,410	9924	74 (5, 37)	12	16 (1, 7)	12	66 (10, 21)	32	41 (6, 22)	21	89 (10, 26)	28

Figure 9

Comparison between indices of fish abundance from different types of longline sets, calculated as the number of fish caught/1000 hooks without regard to capture depth of individual fish ($CPUE_S$). Three types of longline sets were categorized on the basis of the deepest hooks, but every set contained some hooks as shallow as 40–80 m. Data are combined for 1989 and 1990.

Although relatively few mahimahi were captured with timer data, these data indicated maximum abundance was at 40–80 m in 1990 (only one fish was caught on a settled hook in 1989; Fig. 7, Table 4). Pooled data clearly indicated that $CPUE_D$ was highest at 40–120 m (Fig. 8). At >200 m, all mahimahi with timer data were caught on moving hooks.

Examining the $CPUE_S$ data as if the only available depth information were the set type (Fig. 9) made it difficult to correctly qualify the relative abundance of fish in relation to depth. For example, mahimahi appeared almost as abundant in deep sets as in shallow



sets, and spearfish appeared more abundant in very deep than in deep sets, illustrating that it is impossible to correctly describe fish depth distributions without data on catch by hook position, hook depth, and capture time.

Oceanographic habitat

The temperature profile in 1990 (Fig. 10) was representative of the study area in both years, except the bottom of the thermocline (i.e., the 12°C isotherm) was ~40 m deeper in 1989. In both years, the highest catch rate of bigeye tuna with confirmed capture depths occurred at lat. 17°–18°N at 360–400 m in temperatures of 8°–10°C (Fig. 10).

The oxycline in 1990 (Fig. 10) also was similar to that in the previous year (i.e., the 3.0 mg/L isopleth was only 10–20 m deeper in 1989). Most bigeye tuna were caught at DO concentrations of 2–6 mg/L. In both years, the highest catch rate was at 2–3 mg/L.

Figure 10

Temperature and dissolved oxygen profiles of the study area (lat. 14°–20°N, long. 148°–159°W) in 1990 (similar to 1989). Confirmed capture depths of bigeye tuna in 1989 (□) and 1990 (◇) are indicated.

Table 5

Standardized distribution of hooks by depth stratum for four standardized gear types and predicted catch-per-unit-effort (CPUE) for each gear type based on the weighted average observed CPUE by hook depth for five commercially-important species in research longline sets off Hawaii, 1989 and 1990. For each species, relative gear efficiency is given as the ratio between the CPUE for each gear type and for regular gear (too few yellowfin tuna ($N=3$) were caught in 1989 to warrant calculating relative gear efficiency).

Model gear type	Hook number by depth (m)								Bigeye tuna		Yellowfin tuna		Striped marlin		Shortbill spearfish		Mahimahi	
	40-80	80-120	120-160	160-200	200-240	240-280	280-320	Year	CPUE	ratio	CPUE	ratio	CPUE	ratio	CPUE	ratio	CPUE	ratio
	80	120	160	200	240	280	320											
Regular	0	2	2	2	0	0	0	1989	1.93	1.00	0.47		9.30	1.00	5.37	1.00	1.43	1.00
								1990	1.52	1.00	1.36	1.00	4.83	1.00	2.57	1.00	5.03	1.00
								$\bar{x}$	1.73	1.00	0.91		7.07	1.00	3.97	1.00	3.23	1.00
Deep	0	2	2	2	2	2	3	1989	5.95	3.08	0.78		4.85	0.52	3.50	0.65	1.88	1.31
								1990	6.02	3.97	0.88	0.65	2.36	0.49	1.19	0.46	4.45	0.88
								$\bar{x}$	5.99	3.53	0.83		3.60	0.51	2.34	0.56	3.16	1.10
Shallow	2	2	2	0	0	0	0	1989	1.60	0.83	0.47		10.43	1.12	6.83	1.03	3.23	2.26
								1990	0.41	0.27	1.72	1.27	8.12	1.68	3.85	1.50	15.18	3.02
								$\bar{x}$	1.01	0.55	1.09		9.28	1.40	5.34	1.39	9.21	2.64
New	0	0	0	2	2	2	3	1989	7.93	4.10	0.82		2.04	0.22	2.09	0.39	1.76	1.22
								1990	8.42	5.55	0.85	0.63	0.93	0.19	0.61	0.24	3.81	0.76
								$\bar{x}$	8.18	4.82	0.84		1.49	0.20	1.35	0.32	2.78	0.99

The area (lat. 17°–18°N) of highest catch rates for bigeye tuna was on the south edge of a northward transition to a deeper thermocline and oxycline (Fig. 10). The north-south pattern is typical of the central Pacific Ocean at these latitudes, whereas the highly variable pattern in the thermocline between lat. 19.4° and 20°N was probably caused by the proximity to the lee side of the island of Hawaii.

With regard to the other species, the thermal structure of the habitat (Fig. 10) and the confirmed depth distribution of fish (Figs. 4, 7, and 8) suggested that yellowfin tuna were most abundant in the mixed layer (24°–25°C) and the steepest part of the thermocline down to about 15°C. Striped marlin appeared to be most abundant in the mixed layer and the top of the thermocline to ~20°C. Spearfish appeared to occupy a habitat between that of yellowfin tuna and striped marlin, and mahimahi occupied the mixed layer.

Standardized gear efficiency

For bigeye tuna in 1989–90, the CPUE ranges for standardized deep gear and proposed new gear were about 3.1–4.0 and 4.1–5.6 times, respectively, as great as those for regular gear (Table 5). Shallow gear on average was about half as efficient as regular gear in catching bigeye tuna, whereas it was about 40% more efficient than regular gear in catching spearfish and striped marlin. Deep gear was only about half as efficient as regular gear in catching striped marlin and spearfish, and the proposed new gear was only about

20% as efficient for striped marlin and about 30% as efficient for spearfish.

The numbers of yellowfin tuna and mahimahi caught in 1989 were much lower than in 1990, so the latter year provided better data for calculating gear efficiency for these species (Table 5). Shallow gear was about 3.0 times as efficient at catching mahimahi, and deep and new gear reduced efficiency to about 90% and 75% in comparison with regular gear. For yellowfin tuna, shallow gear was about 25% more efficient than regular gear, whereas the deep and new gear types were each about 65% as efficient.

Discussion

Habitat depth

Hook timers are useful in confirming whether fish are caught while longline hooks are sinking, settled, or rising. Combined with capture depths from TDRs, hook timers offer a new method for establishing the habitat depth of large pelagic fishes. Stock assessments (Suzuki 1989) depend on the estimation of effective effort, defined as fishing effort corrected for differences in efficiency due to gear and habitat depth (Suzuki et al. 1977). Improving the definition of tuna and billfish habitats and the estimation of effective effort in those habitats should lead to significant improvements in assessing true abundance.

Comparisons of CPUE by two gear types provide only qualitative information on habitat depth. For

example, since deep gear is more efficient than regular gear for bigeye tuna, this species must occupy a relatively deep habitat (Suzuki et al. 1977). More specific information on habitat depth is provided by catches and CPUE_H by hook position (Hanamoto 1979 and 1987, Hanamoto et al. 1982, Suzuki and Kume 1982), especially when TDRs are used to record gear depth (Saito 1973 and 1975, Hanamoto 1974, Nishi 1990). Capture depth estimates without TDR records ignore major variations in actual gear depth (Fig. 2; Nishi 1990), and those without hook timers are biased by the inclusion of inappropriate hook depths.

A possible source of bias in the present study is the inclusion of some falsely confirmed depths due to fish being caught with timers already activated. The proportion of false estimates should be similar to the frequency of timers that were without fish and were triggered while settled, which was only 3.9% in 1989 and 2.6% in 1990 (Table 3). Thus it is unlikely that >4% of confirmed capture depths in this study are incorrect because of false timer readings.

Many pelagic longline studies (Saito 1975, Hanamoto 1976, Yang and Gong 1988) assume that fish are caught while hooks are at settled depths. Supporting this assumption, Saito (1973) has shown that albacore *Thunnus alalunga* are caught almost exclusively by settled hooks, based on capture times indicated by fluctuations in TDR records. Using hook timers, the present study adds new information: Almost 90% of bigeye and yellowfin tuna also are caught while hooks are at settled depths (Table 4). However, hook timers indicate this generalization does not extend to striped marlin, spearfish, mahimahi (Table 4), and most of the commercially unimportant species (Fig. 5). Although most of these fish are also caught on settled hooks, a substantial fraction are not, and this must be considered when quantifying their depth ranges (Fig. 4).

Besides the present study, little information exists on longline capture depths for mahimahi, spearfish, and striped marlin. In the study area, CPUE_D values for these species (Fig. 7) indicate maximum abundance at depths in the mixed layer for mahimahi (<100 m, 24°–25°C; Fig. 10), extending into the top of the thermocline for striped marlin (120 m, 20°C) and into the middle of the thermocline for spearfish. Striped marlin are reported to be caught most frequently on longline hooks closest to the surface (60–90 m) in the eastern tropical Pacific and Indian Oceans, but they may be more abundant above this depth (Hanamoto 1979, Hanamoto et al. 1982). Mahimahi and spearfish may also be more abundant above the uppermost stratum (40–80 m) in the present study, since their catch rates appear to increase towards the surface (Fig. 7).

Striped marlin are also reported caught on deep longline hooks (~200 m; Hanamoto et al. 1982) and at

the deep end of vertical longline gear (336 m; Saito 1973); but in the present study, their deepest confirmed capture depth is 210 m. Tracking data on striped marlin off California indicate a shallow (<60 m) depth distribution with most of the daytime spent within 10 m of the surface (Holts and Bedford 1989).

The depth distribution (200–400 m) of bigeye tuna in the present study is deeper than in many previous reports (Hanamoto 1974, 50–160 m; Saito 1975, 207–245 m; Suzuki and Kume 1982, 170–300 m; Yang and Gong 1988, 260–300 m; Nishi 1990, 140–180 m), although these studies have found bigeye tuna are most abundant on the deepest hooks fished. Hanamoto (1987) hypothesizes a habitat depth of 250–400 m for the central Pacific Ocean at latitude 25°N, based on the observed maximum longline CPUE at temperatures of 10°–15°C. The highest CPUE_D values in the present study are at the cold, deep end of this range (Fig. 7), deeper than most hooks used in commercial fishing gear. However, the CPUE_D value at 280–400 m is not significantly different from that at 200–400 m (Fig. 8). Although these results may be specific to January and February, perhaps commercial CPUE could be improved by increasing fishing depth, at least during winter months.

Seasonal and geographic variation in temperature and DO profiles may affect the depth preferences of pelagic fish. Hanamoto (1975, 1987) has hypothesized that the deep end of bigeye tuna habitat is limited by DO concentrations below 1 mL/L (1.4 mg/L) and by temperatures below 10°C. Results of the present study suggest that bigeye tuna are seldom caught in waters with a DO concentration of ~<2 mg/L (Fig. 10). Oxygen concentrations of ~2–3 mg/L cause significant reductions in bigeye tuna cardiac output (1.9–2.6 mg/L) and heart rate (2.7–3.5 mg/L), suggesting that bigeye tuna cannot maintain a full range of activity at lower DO concentrations (Bushnell et al. 1990).

Longline data to support the hypothesis of a 10°C temperature limit independent of the DO limit are sparse. Few hooks have been deployed in waters colder than 9°–10°C with DO concentrations of >1 mL/L (Hanamoto 1975, 1987). In the present study, the only area with DO values >2 mg/L and temperatures <8°C was at lat. 10°–20°N (Fig. 10). Currents prevented hooks from reaching cold (6°–8°C) water in this area.

Sonic tracking of bigeye tuna around Hawaii indicates a depth distribution slightly shallower than that in longline studies (Hanamoto 1987, 250–400 m; present study, 200–400 m). Holland et al. (1990) have reported that tracked bigeye tuna spend most of the daytime at 200–240 m in 14°–17°C water. This may be due to the association of the tracked bigeye tuna with fish aggregating devices or due to a size-related difference. The 72- to 74 cm bigeye tuna studied by Holland

et al. (1990) weighed ~ 10 – 12 kg, whereas longline-caught bigeye tuna in the present study averaged >30 kg.

Results of the present study apply predominantly to daytime habitat depths, but an important difference apparently exists between the daytime and nighttime depth distributions of bigeye tuna (Holland et al. 1990). At night, tracked bigeye tuna move upward to ~ 70 – 90 m at temperatures of 23° – 25° C. Confirmation of this nocturnal behavior comes from a new nighttime longline swordfish fishery that has recently developed in Hawaii using chemical light sticks. Although this fishery deploys very shallow (generally <90 m) gear, the bycatch of bigeye tuna is surprisingly high (S. Pooley, NMFS Honolulu Lab., pers. commun., April 1991), indicating that bigeye tuna have a shallow nighttime depth distribution.

The small number of yellowfin tuna caught in this study makes estimated habitat depth (40–200 m) less certain, but it does not differ much from the 90–230 m depth found in Suzuki and Kume (1982) and Yang and Gong (1988). Tracking studies (Carey and Olson 1982, Holland et al. 1990) show yellowfin tuna spend most of their time at depths <100 m. Depths of the highest longline CPUE_D for yellowfin tuna in the present study (40–80 m; Fig. 7) are similar to the depths (30–80 m) at which tracked yellowfin tuna in Hawaii spend over 50% of their time during the day (Holland et al. 1990), tending to confirm that yellowfin tuna habitat is mostly in the mixed layer.

Methods for estimating habitat depths in the present study could be improved by increasing the number of TDRs deployed or by developing a model, calibrated with TDRs, to predict gear depth based on wind and current measurements, divergence or convergence of floats, and stops and starts in deployment and retrieval. Procedures to estimate the capture depths of fish caught while hooks are sinking or rising could also be developed, but would depend on very accurate time-keeping, since the gear rises rapidly during retrieval (Fig. 3).

Catch by moving hooks

The catch of shallow-swimming species on deep hooks moving through shallower depths could reduce the selectivity of gear designed to catch deep-swimming species. The results show that moving longline hooks are more effective (per unit time) than settled hooks at catching billfish, mahimahi, some sharks, and most other non-tuna species. However, the majority of these fish are caught on settled hooks, because of the longer time that hooks are settled (Fig. 5). The relative amount of time hooks are moving vs. settled is the only aspect of the commercial daytime tuna longline opera-

tions that differs much from the fishing method used in this study. The gear is left in the water longer and then retrieved more rapidly during commercial fishing, so hooks spend less time moving and more time settled. This may result in greater proportions of fish being caught on settled hooks by commercial fishermen than in the present study.

Eliminating shallow-settled hooks should greatly reduce the catch of shallow-swimming species. For non-tuna species, deploying and retrieving the gear less often (as in commercial operations) should decrease the CPUT (catch-per-unit-time), but would increase the CPUE because the latter increases with set duration. In contrast, bigeye tuna CPUT and CPUE should increase with less frequent deployment and retrieval, because CPUT is highest for settled hooks.

The mechanism for increased CPUT on moving hooks for non-tuna species is unclear. Moving bait may be more attractive than settled bait, but the low number caught on sinking hooks (Fig. 5) suggests that gear motion alone is not responsible for increased catch rate. Perhaps a gradual aggregation of fish around the gear (or the vessel) while the gear is settled contributes to the catch rate by rising hooks.

Although hook timer data provide a reliable way to confirm when fish are caught on settled hooks, such data may be less reliable as a measure of fish caught on moving hooks, because of the uncertainty regarding fish with timers triggered at recovery (Fig. 5). These fish are not included in the number captured on moving hooks (Table 4); their timer readings cannot be distinguished from ones triggered after being brought aboard. Therefore, the estimates of fish caught on moving hooks (Table 4) may be too low. Alternatively, if these readings indicate a tendency for some fish to not activate timers until they struggle during recovery, then the estimates of fish caught on moving hooks may be too high. In either case, only inferences regarding CPUT on moving and non-moving hooks, and the estimated proportions of fish caught on moving hooks, are affected by this uncertainty. The estimates of catches on non-moving hooks are conservative, and confirmed capture depths are not affected.

The higher proportion of fish caught on moving hooks in 1989 compared with 1990 (Table 4) could have been caused by moving hooks being less visible in 1990, since branch lines were more often recovered after dark (Table 1). Sets also lasted longer in 1990 (Table 1); this may have increased the relative proportion of catches on settled vs. moving hooks. The CPUT in relation to sinking, settled, and rising gear, and to the time of day, should be explored further using the techniques developed in the present study.

A TDR attached to vertical and regular rope longline gear sometimes records abrupt depth changes as a fish

is caught, making the TDR equivalent to a hook timer if it is close to a branch line that catches a fish (Saito et al. 1970, Saito 1973, Yamaguchi 1989). The records of TDRs at positions close to fish caught with hook timers in the present study were checked to see whether they indicated the time of capture, but the depth of the monofilament longline gear was much less stable (Fig. 3) than in the depth records of Saito et al. (1970), Saito (1973), and Yamaguchi (1989) using TDRs on rope gear. On monofilament longline gear, frequent depth changes resembling fish captures occur even when no fish are caught, making TDRs unreliable as substitutes for hook timers.

Viability of released fish

Before the present study, it was believed that fish would survive only a few hours after capture on longline gear (Grudinin 1989, Yamaguchi 1989) despite large pelagic species being known to survive capture and release from other types of gear (Foreman 1987, Squire 1987, Holts and Bedford 1989). Commercial longline fishermen in Hawaii speculated that much of their catch was made as hooks were sinking or rising, because most were alive or appeared long dead (F. Amsberg, Der Fischen Co., Honolulu, HI 96822, pers. commun., March 1988). Based on TDR data from fish on regular longline gear (Yamaguchi 1989), vertical movements stop 1.0–1.5 h after capture for yellowfin tuna, 1.5–4.0 h for bigeye tuna, and ~0.5 h for spearfish and shark. This cessation of vertical movement has been interpreted as death (Yamaguchi 1989). Grudinin (1989) has reported on the diurnal periodicity of bigeye and yellowfin tuna catch rates based on the proportion recovered alive, assuming that tuna survive ≤ 2 h on longline gear. However, hook-timer results (Fig. 6) show that fish survive much longer than this, suggesting that vertical movement is not a reliable indicator of survival. Alternatively, the results of the present study could be specific to monofilament gear, which could have less resistance to moving through the water than does rope gear.

Clearly the high proportion of live fish (Table 2) is not primarily the result of capture during the 0.5 h rising period. The viability of longline-caught fish is indicated by their hooked longevity and the recovery of tagged fish. As a management option, non-retention of striped marlin and spearfish could reduce fishing mortality due to longline fishing. The importance of the reduction would depend on the length of the fishing operation; but in the present study, longline fishing mortality for striped marlin could have been reduced by 70% (Table 2) if all live fish had been released and had survived.

Gear efficiency and selectivity

Gear efficiency, defined as the dimensionless ratio of the CPUE of one gear type (i.e., deep gear) divided by the CPUE of the regular gear type, is the factor used to calculate effective effort by gear fishing at different depths (Suzuki et al. 1977). Total effective effort can then be used to calculate indices of relative abundance and to model stock production (Suzuki 1989). The most thorough approach thus far has been to calculate gear efficiency by area and season (Suzuki and Kume 1982). A better understanding of the variables that alter habitat depth would permit gear efficiency to be predicted as a function of environmental conditions, and help account for variation in abundance indices caused by environmental anomalies.

The relative efficiency of standardized deep gear (Table 5) follows the pattern observed in previous studies (Suzuki et al. 1977, Yang and Gong 1988) in which deep gear is more efficient at catching bigeye tuna and less efficient at catching yellowfin tuna and istiophorid billfish. However, the estimated efficiency of the standardized deep gear for bigeye tuna in the present study is greater (ratio 3.1–4.0 over the 2 years; Table 5) than that reported by Suzuki et al. (1977) for the central and western equatorial Pacific (1.8) or by Yang and Gong (1988) for the Atlantic (1.9). Suzuki and Kume (1982) have presented graphs of deep and regular CPUE for bigeye tuna on a quarterly basis by area throughout the Pacific, and these data indicate very little difference between gear types in the central Pacific north of lat. 15°N. The high efficiency estimated for deep gear in the present study may partly result from using measured depths rather than inferred depths to define deep and regular gear types. Also, a high relative efficiency for deep gear may be specific to the Hawaii area in the winter season.

The relative efficiency of deep gear for yellowfin tuna in the Atlantic (0.95, Yang and Gong 1988) is greater than in the central and western equatorial Pacific (0.73, Suzuki et al. 1977) and in the present study (0.65, Table 5). Relative efficiency of deep gear for striped marlin in the central and western equatorial Pacific (0.28, Suzuki et al. 1977) is much lower than in the central Pacific north of Hawaii (0.74, Suzuki 1989), nicely bracketing the estimate from the present study (0.51, Table 5).

The model estimates of gear efficiency (Table 5) are not meant to supplant earlier estimates based on much larger data sets (Suzuki et al. 1977, Suzuki and Kume 1982, Yang and Gong 1988, Suzuki 1989), but rather to show how catch by hook position can be used to estimate CPUE by different gear configurations, especially hypothetical configurations for which no real data exist. Efficiency estimates (Table 5) suggest that

shallow sets of the type hypothesized to represent early use of monofilament longline gear in Hawaii would be expected to catch about 40% more billfish and 160% more mahimahi than would regular longline gear. Large increases in longline catches of these fish in Hawaii have occurred in recent years (1989-90, Boggs 1991) as the expanding Hawaii fishery adopted a new type of gear. The proposed new gear configuration would be an effective way to reduce the catch of spearfish and striped marlin by ~70-80% below that of regular gear.

Hook timers and TDRs are useful in documenting the depth distribution and habitat of pelagic fish and in showing how different configurations of longline gear and the release of live fish can be effective means of reducing fishing mortality for some species. Better methods of identifying the habitats of pelagic fishes should make it easier to estimate real changes in fish abundance by accounting for changes in fishing methods and the environment.

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GLOBAL POPULATION STRUCTURE AND NATURAL HISTORY OF THE GREEN TURTLE (*CHELONIA MYDAS*) IN TERMS OF MATRIARCHAL PHYLOGENY

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Abstract.—To address aspects of the evolution and natural history of green turtles, we assayed mitochondrial (mt) DNA genotypes from 226 specimens representing 15 major rookeries around the world. Phylogenetic analyses of these data revealed (1) a comparatively low level of mtDNA variability and a slow mtDNA evolutionary rate (relative to estimates for many other vertebrates); (2) a fundamental phylogenetic split distinguishing all green turtles in the Atlantic-Mediterranean from those in the Indian-Pacific Oceans; (3) no evidence for matrilineal distinctiveness of a commonly recognized taxonomic form in the East Pacific (the black turtle *C.m. agassizi* or *C. agassizi*); (4) in opposition to published hypotheses, a recent origin for the Ascension Island rookery, and its close genetic relationship to a geographically proximate rookery in Brazil; and (5) a geographic population substructure within each ocean basin (typically involving fixed or nearly fixed genotypic differences between nesting populations) that suggests a strong propensity for natal homing by females. Overall, the global matriarchal phylogeny of *Chelonia mydas* appears to have been shaped by both geography (ocean basin separations) and behavior (natal homing on regional or rookery-specific scales). The shallow evolutionary population structure within ocean basins likely results from demographic turnover (extinction and colonization) of rookeries over time frames that are short by evolutionary standards but long by ecological standards.

Key words.—Biogeography, *Chelonia agassizi*, *Chelonia mydas*, conservation genetics, mitochondrial DNA, molecular clock, molecular systematics, natal homing.

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The green turtle (*Chelonia mydas*) has a complex life history that is difficult to study directly because of the large spatial and temporal scales involved. Hatchlings and juveniles move among several habitats during development, adults migrate between feeding and nesting grounds that are hundreds

or thousands of kilometers apart, and both movements are difficult to track in the marine environment (Carr, 1980). Because only females ascend nesting beaches, much of what is known about the life history of marine turtles has come from tagging experiments on nesting females. Aspects of green turtle biology less amenable to direct observation have yielded to indirect (and often ingenious) methods. Reproductive histories

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have been studied with laparoscopy (Limpus and Reed, 1985), general migratory behaviors have been deduced from the growth patterns and species compositions of the epibiota on turtle carapaces (Eckert and Eckert, 1988), and turtle growth rates have been assessed by osteology and histology (Rhodin, 1985; Zug et al., 1986; Klinger and Musick, 1992). Another approach that may uncover otherwise intractable aspects of the natural history and evolution of marine turtles involves the assay of molecular genetic markers. In this study we employ mitochondrial (mt) DNA restriction site data to analyze matriarchal phylogeny and female-mediated gene flow among populations of *Chelonia mydas* from around the world.

The herbivorous green turtle inhabits tropical and subtropical feeding pastures in every major ocean basin. At intervals of 2 to 10 or more years, each mature female migrates from feeding grounds to a nesting locale, following routes that span hundreds or thousands of kilometers (Meylan, 1982). Green turtles nest colonially; in many locations, females utilize specific beaches while adjacent habitat remains unvisited (Carr and Carr, 1972). During a single nesting season, a female typically lays two to seven clutches of about 100 eggs each before returning to feeding grounds. Hatchlings emerge after an incubation period of eight weeks and enter an oceanic habitat where they may remain for several years (Carr, 1987). Juveniles eventually recruit to neritic foraging habitats and switch to the primarily herbivorous adult diet (Pritchard, 1976). Published estimates of first age at sexual maturity range from 27 to 33 years in the Atlantic (Frazer and Ladner, 1986), 30 or more years in Australia (Limpus and Walter, 1980), and 9 to 58 years in Hawaii (Balazs, 1982; see also Zug and Balazs, 1985).

Tagging data have demonstrated that mature females return quite faithfully to the same rookery for nesting in successive seasons (Carr and Ogren, 1960). This site fidelity led Carr (1967) and others to propose that adult females return to nest at their natal rookery. Hendrickson (1958) and Owens et al. (1982) proposed an alternative scenario also consistent with the nest-site fidelity of adult females. Under their "social facilitation" hypothesis, first-time breeders

follow experienced females to a nesting beach, and having had a "favorable" experience, fix on that site for future nesting. These hypotheses have proved difficult to test directly, as no known tag will persist through the transition from a 40 g hatchling to a 100 to 200 kg adult (Carr, 1986). Philopatry to natal site does, however, generate the testable prediction that rookeries should exhibit genetic differentiation with respect to female-transmitted traits (such as mtDNA), whereas social facilitation would allow high rates of female-mediated gene flow between rookeries that share feeding grounds. Tagging data indicate that nesting adults typically return to the same feeding grounds (Limpus et al., 1992), and these feeding pastures often are shared by turtles from several rookeries (Pritchard, 1976). This cooccupation of feeding pastures by females from different rookeries allows critical genetic tests of the social facilitation hypothesis.

In addition to contemporary behavioral components of population genetic structure, mtDNA analyses should reveal geographical and historical aspects of green turtle dispersal. Even if natal homing predominates, migrational "mistakes" must have occurred to account for the widespread distribution of rookeries. How high is intercolony gene flow within ocean basins, and what are the historical relationships among nesting colonies? Furthermore, the tropical and subtropical distribution of green turtles may prohibit gene flow between Atlantic and Indian-Pacific populations. When were these populations last connected?

mtDNA analysis may also demonstrate whether genetic partitions in the matriarchal phylogeny of green turtles agree with the putative population subdivisions and taxonomic units suggested from behavioral and morphological evidence. Basic life-history features are shared by all green turtle populations, but colonies show much variability in details of ethology and morphology (Mrosovsky, 1983). While describing these differences between regional populations, earlier researchers pondered the extent to which they reflect genetic or evolutionary divergence (Carr and Goodman, 1970). Opinions range from speculation that each nesting population is a distinct taxon-

nomic entity, to the possibility that essentially no evolutionary distinction exists even between populations in separate ocean basins (review in Mrosovsky, 1983; see also Bonhomme et al., 1987).

Finally, all of these issues are relevant to conservation efforts for this endangered species. In recent reports, mtDNA data on endangered species have proved useful for resolving population groupings in cases where morphological analyses were controversial or inconclusive (Avice, 1989; Bowen et al., 1991). Green turtles have been utilized widely by coastal cultures for thousands of years, but overharvesting in the last four centuries has driven several populations to extinction and has greatly diminished others (Parsons, 1962). Knowledge of the degree of demographic and evolutionary independence among rookeries is critically important to future management plans. As noted by Carr (1975), "It seems clear that if *Chelonia* is to get its share of concern as a group of vulnerable, threatened, and endangered forms of life, the composite nature of the *mydas* complex must be made known to conservationists and legislative governments." With these many issues in mind, we conducted the following global survey of green turtle rookeries.

MATERIALS AND METHODS

Biological Samples

Samples from 226 different nests were taken from the 15 Atlantic, Mediterranean, Indian, and Pacific Ocean nesting locations described in Table 1 and Figure 1. Sample sizes and locations were dictated by permit limitations as well as by biological criteria. International field collections typically required four to six permits and 6 to 18 months of advance correspondence. The nations and territories included in this study represent a subset of targeted locations for which permit agencies were accessible and receptive to biological research.

In deference to the endangered status of *C. mydas*, the sampling strategy was designed to minimize impact on natural populations. The high natural mortality of eggs and hatchlings made these the best candidates for collection. From each sampled nest, one hatchling or two eggs were taken. Two

eggs were necessary to offset mortality during transportation, as embryos are very sensitive to motion during the first few weeks of development (Limpus et al., 1979). Eggs were incubated for two to eight weeks before processing. Hatchlings were processed immediately following euthanasia. Because nestmates are normally expected to be identical in mtDNA genotype, the reported sample sizes refer to the number of different nests assayed.

Laboratory and Data Analysis Procedures

Closed-circular mtDNA was isolated from soft tissues (hatchlings) or whole embryos (eggs) by CsCl-ethidium bromide density gradient centrifugation (Lansman et al., 1981). Purified mtDNAs were digested with the 17 informative four-, five- and six-base cutting restriction enzymes listed in Table 2. In addition, representative samples were digested with *Ava*I, *Bam*HI, *Bgl*II, *Bgl*III, *Bst*EII, *Cla*I, *Kpn*I, *Nsi*I, *Pst*I, *Sac*I, *Sal*I, and *Xba*I, but these enzymes proved to be phylogenetically uninformative, producing either one or no cuts in our assays. Digestion fragments were end-labeled with ³⁵S nucleotides and separated on 1.0 to 1.7% agarose gels. When restriction changes involved small (<0.5 kb) fragments, patterns were confirmed using 5% acrylamide gels. Restriction fragments were visualized by autoradiography and assigned molecular weights on the basis of comparison to a 1-kb standard.

Estimates of nucleotide sequence divergence (*p* values) were calculated by the "site" approach of Nei and Li (1979), and haplotype and nucleotide diversities as defined by Nei and Tajima (1981) and Nei (1987). Relationships among mtDNA genotypes were assessed by UPGMA clustering (Sneath and Sokal, 1973), and by an exhaustive search of branching networks using parsimony criteria (Swofford and Olsen, 1990) in the computer program PAUP (version 3.0; Swofford, 1990). Statistical support for branches in the parsimony network were examined by bootstrapping 100 replicates (Swofford, 1990). Restriction fragment profiles were characterized with composite letter codes and these were joined into a par-

TABLE 1. Sample locations and population information.

Rookery location	N	Rookery size (females/year)	Feeding grounds	Comments	Refs.
ATLANTIC					
1) Ascension Is- land, UK	35	1,600–3,000	Brazilian Coast	Collections made in 1987 (N = 15) and 1990 (N = 20)	1
2) Atol das Rocas, Brazil	16	50–100	Unknown but probably includes Brazilian Coast	Appears to be declin- ing	2
3) Matapica, Suri- name	15	a few thousand	Brazilian Coast		3
4) Tortuguero, Costa Rica	15	5,000–23,000	Western Caribbean, pri- marily on coast of Nicaragua	Largest west Atlantic rookery	4
5) Aves Island, Venezuela	8	300–500	Caribbean, including Nicaragua	Declining	5
6) Hutchinson Is- land, FL USA	24	a few hundred along east coast of Florida	Unknown but probably includes Gulf of Mex- ico and Caribbean	Collections made in 1986 (N = 10) and 1990 (N = 14)	6
7) Pailoa, Guinea Bissau	13	about 400	Unknown		7
MEDITERRANEAN					
8) Lara Bay, Aka- mas Peninsula, Cyprus	10	fewer than 100	Mediterranean	Severely depleted by overfishing; may complete life cycle in Mediterranean	8
INDIAN OCEAN					
9) Ras Al Hadd, Oman	15	about 6,000	Gulf of Oman, Gulf of Aden, Red Sea		9
PACIFIC OCEAN					
10) Heron Island, Queensland, Australia	15	several thousand at Heron and adjacent cays	Arafura and Coral Seas to Vanuatu and Fiji	Primary nesting site in southern Great Barrier Reef	10
11) Ogasawara Ar- chipelago, Ja- pan	20	200–400	Pacific side of Japanese Archipelago and East China Sea	Largest rookery in northwest Pacific	11
12) French Frigate Shoals, Hawaii	22	100–500	Extend to both ends of archipelago	Collections made in 1986 (N = 12) and 1990 (N = 10); may complete all or most of life cycle within archipelago	12
13) Mopelia Atoll, French Polyne- sia	3	a few hundred	includes Fiji, New Cale- donia, and Tonga		13
14) Michoacan, Mexico	7	1,000–3,000	Baja California, Central America, South America	Drastic decline in re- cent decades	14
15) Isabela Island, Galápagos, Ec- uador	8	1,200–3,500 in ar- chipelago	Costa Rica to Peru	May include resident and migratory tur- tles	15

1) Mortimer and Carr, 1987; Carr, 1975; 2) M. Marcovaldi, pers. comm.; Groombridge and Luxmoore, 1989; 3) Schulz, 1982; Pritchard, 1976; 4) Carr et al., 1978; 5) Sole and Medina, 1989; Pritchard and Trebbau, 1984; 6) Conley and Hoffman, 1987; 7) T. Agardy, pers. comm.; 8) Demetropoulos and Hadjichristophorou 1989; Demetropoulos and Hadjichristophorou 1987; Groombridge, 1988; 9) Ross and Barwan, 1982; Ross, 1985; 10) Limpus, 1982; Limpus et al., 1991; 11) H. Suganuma, pers. comm.; Suganuma, 1985; 12) Balazs, 1976, 1980, and unpubl. data; 13) Pritchard, 1982; Lebeau, 1985; Meylan, 1982 and references therein; 14) Clifton et al. 1982; Alvarado and Figueroa, 1990; 15) Green, 1983; Green, 1984; Pritchard 1971.

simony network that interrelates observed restriction fragment patterns.

Because we are interested both in mean levels of divergence between rookeries and

genetic relationships of particular pairs of colonies (e.g., those that are adjacent, or share feeding grounds), some of the analyses described below include pairwise rookery

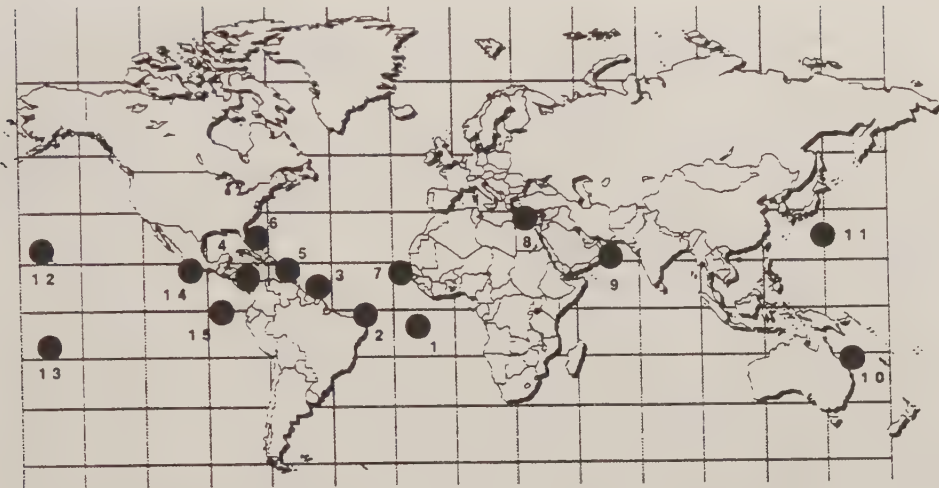


FIG. 1. Collection locales for *Chelonia mydas*. Numbers refer to localities described in Table 1.

comparisons (although results of pairwise comparisons are not independent). Pairs of rookeries were tested for significant differences in haplotype frequency by the *G* test with Yates' correction for small sample size

(Sokal and Rohlf, 1981). The cladistic approach of Slatkin and Maddison (1989) was used to generate pairwise estimates of Nm (where N is the size of each local population and m is the migration rate). In cases where

TABLE 2. Description and distribution of the 14 distinct mtDNA genotypes observed in green turtles collected at 15 rookeries. Italicized letters refer to mtDNA digestion profiles produced by (from left to right): *AvaII*, *BclI*, *BstNI*, *DdeI*, *DraI*, *DraII*, *EcoRI*, *EcoRV*, *HindII*, *HindIII*, *MboI*, *MspI*, *NdeI*, *PvuII*, *SpeI*, *SstII*, and *StuI*. Adjacent letters in the alphabet indicate that fragment profiles differ by a single restriction site; nonadjacent letters differ by at least two sites, with the exception of the *MspI* profiles in which A, B, and D differ from C by single restriction sites.

Code	mtDNA genotype	Rookery location	Number of nests
A	ACCCCCCCCCCCCCDCC	Florida, USA	21
		Tortuguero, Costa Rica	15
		Aves Island, Venezuela	1
B	ACCCBCCCCCCCCDCC	Florida, USA	3
C	ACCCCCCBCCCCCCCC	Matapica, Suriname	15
		Aves Island, Venezuela	7
D	ACCCCCCCCCCCCCCCC	Ascension Island, UK	34
		Atol das Rocas, Brazil	15
E	ACCCCCCCCCCCCCCCD	Ascension Island, UK	1
F	BCCCCBCCCCCCCCCCC	Atol das Rocas, Brazil	1
G	ACCCCBCCCCCCCCCCCC	Pailoa, Guinea Bissau	13
H	ACCCCCCCCCDCCCCC	Lara, Cyprus	10
I	CCCCCBDCCCCCDBBCC	Ras Al Hadd, Oman	15
		Galapagos, Ecuador	8
		Michoacan, Mexico	7
		Hawaii, USA	6
J	CCCCBECCCCDBBCCD	Hawaii, USA	16
K	BCCCCBECCCCACBBCC	French Polynesia	2
L	CCCCBDCCCCBCBBCC	Queensland, Australia	15
		French Polynesia	1
		Ogasawara Island, Japan	1
M	CCCCBDCCCCDBBCC	Ogasawara Island, Japan	5
N	DCCCCBDCCCCCBCC	Ogasawara Island, Japan	14

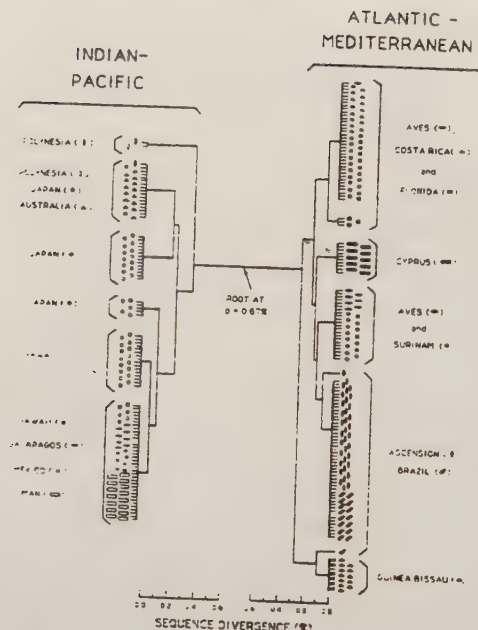


FIG. 2. UPGMA phenogram summarizing relationships among the 226 sampled nests of the green turtle. Note that to conserve space, the sequence divergence axes on the bottom are presented as mirror images centered around the placement of the root. The fundamental distinction between Atlantic-Mediterranean versus Indian-Pacific assemblages was also evidenced by strong bootstrap support (97% level) in parsimony analyses based on a presence/absence site matrix.

no genotypes were shared, an upper bound on the point estimate of $Nm = 0$ was calculated by the approach described by Slatkin (1989). Pairwise estimates of Nm within each ocean basin were also calculated from G_{st} values ($Nm = 1/2(1/G_{st} - 1)$)—Takahata and Palumbi, 1985). Finally, estimates of mean migration rate among rookeries within each ocean basin were calculated by the private-allele method (Slatkin, 1985), using the parameters and equation in Slatkin and Barton (1989). Due to small sample size, the Polynesia rookery data were excluded from pairwise comparisons (G test and Nm estimates).

RESULTS

A total of 14 distinct mtDNA haplotypes was observed among the 226 green turtles (Table 2), in assays that involved a mean

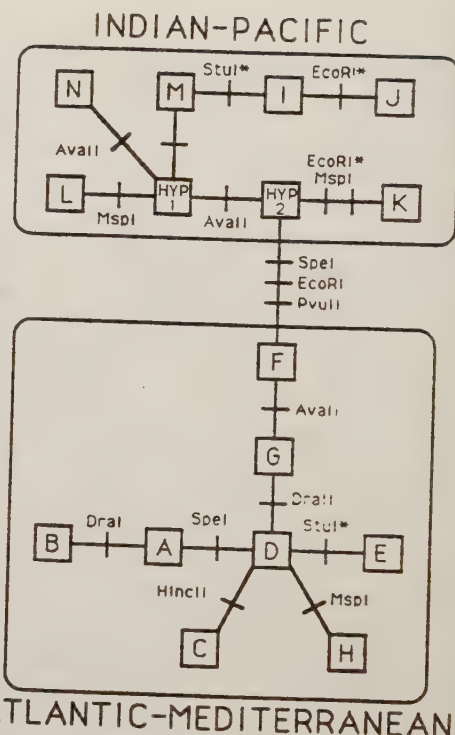


FIG. 3. Parsimony network summarizing the interrelationships among the mtDNA fragment profiles, which are lettered as in Table 2. "Hyp 1" and "Hyp 2" represent hypothetical genotypes not observed in the current survey. Enzymes responsible for fragment pattern changes are indicated along branches, and the stars next to *StuI* and *EcoRI* indicate the only two instances in which homoplasy (convergent evolution to a common fragment pattern) has been assumed.

of 109 restriction sites scored per individual. Digestion profiles for all enzymes are presented in Bowen (1992). All restriction fragment changes could be accounted for by the gain or loss of particular restriction sites. Considered altogether, haplotypic and nucleotide diversities in the green turtle survey were 0.874 and 0.002, respectively.

Global Phylogeography

A striking feature of the mtDNA data is the phylogenetic grouping of observed haplotypes into two assemblages that correspond exactly to major oceanic basins: (1) the Atlantic Ocean and Mediterranean Sea; and (2) the Indian and Pacific Oceans (Figs. 2 and 3). All individuals from these two groups were separated by five or more re-

striction site changes (Fig. 3). Net nucleotide sequence divergence estimated between oceans (after correction for within-ocean variability) was $p_{\text{corr}} = 0.0060$. The interoceanic distinction is evident in both the UPGMA analysis (where the clusters join at $p = 0.0067$), as well as in the parsimony analyses (where bootstrap support was at the 97% level).

Intraoceanic Gene Flow

Within the Atlantic-Mediterranean assemblage ($N = 136$), eight different mtDNA genotypes were observed among the eight assayed rookeries (Fig. 3). Haplotypic and nucleotide diversities were 0.764 and 0.0005, respectively. Genotype frequencies differed significantly in 25 of 28 pairwise rookery comparisons (Table 3A), and many of these involved fixed haplotype distinctions in our samples (Table 2).

Within the Indian-Pacific assemblage ($N = 90$), six different genotypes were observed among the seven assayed colonies (Fig. 3). Haplotypic and nucleotide diversities were 0.753 and 0.0008, respectively. Although two common genotypes ("I" and "L" in Table 2) were shared by several widely separated rookeries, genotype frequencies nonetheless differed significantly in 12 of 15 pairwise rookery comparisons (Table 3B).

Table 4 summarizes estimates of inter-rookery gene flow (Nm) within the Atlantic-Mediterranean and Indian-Pacific groupings, based on Slatkin's (1989) cladistic approach and Takahata and Palumbi's (1985) G_{st} estimator. Most such values proved to be less than 1.0, indicating very little intercolony gene flow through females. Mean intraocean migration estimates based on the private allele approach are also consistent with this conclusion: $Nm \approx 0.3$ for Atlantic-Mediterranean rookeries and $Nm \approx 0.2$ for Indian-Pacific rookeries. In only the few cases where we could not distinguish rookeries in our assays were gene flow estimates higher (Tables 3 and 4). [We are skeptical that such colonies truly experience high contemporary gene flow, because (a) our assays may have failed to detect haplotype differences that do exist; and (b) these results might be due to recent historical connectedness—see below.]

In general, values for Nm greater than

approximately 1 to 4 indicate that gene flow is sufficiently high to maintain a relatively homogeneous mtDNA gene pool, whereas lower values indicate that gene flow is unlikely to retard genetic divergence of isolated gene pools by genetic drift (Slatkin, 1987; Birky et al., 1983). However, some caveats concerning these estimators should be mentioned. First, in this study these estimates are based on a single gene (mtDNA) genealogy. More precise estimates of migration rates would be expected from data involving multiple independent gene genealogies, where sampling errors introduced from single-locus estimates would be reduced. Second, assumptions of population equilibrium underlying some of these estimates of Nm may not be met. Last, the theoretical basis for these estimates has been developed only recently (Slatkin and Barton, 1989), and empirical calibrations currently are unavailable. Although Nm estimates from haploid data are useful for drawing qualitative conclusions, specific quantitative comparisons of Nm values should not be overinterpreted.

DISCUSSION

Global Matriarchal Phylogeny and mtDNA Rate Calibration

Phylogenetic relationships among mtDNAs from 15 globally distributed green turtle rookeries indicate a historical bifurcation of the *Chelonia mydas* complex into (1) the Indian and Pacific Oceans, and (2) the Atlantic Ocean and Mediterranean Sea. This genetic pattern is consistent with the geographic and climatic boundaries that currently define green turtle distributions. Populations from these two regions probably are isolated by the cold temperate conditions around the southern tips of Africa and especially of South America, whereas no physical barriers to movement now exist within the Atlantic-Mediterranean or within the Indian-Pacific Ocean basins. Thus the data from mtDNA lineages indicate that the geographic partitioning of the world's oceans by continental landmasses has been of overriding significance in shaping the global matriarchal phylogeny of *C. mydas*.

The overall magnitude of mtDNA sequence divergence in green turtles is low

TABLE 3. G tests of significance for haplotype frequency differences among green turtle rookeries.

A. ATLANTIC OCEAN AND MEDITERRANEAN SEA							
	I	II	III	IV	V	VI	VII
I Florida, USA	—	G = 0.7 NS	G = 21.0 P < 0.001	G = 42.7 P < 0.001	G = 69.6 P < 0.001	G = 44.5 P < 0.001	G = 38.9 P < 0.001
II Tortuguero, Costa Rica		—	G = 16.2 P < 0.001	G = 32.8 P < 0.001	G = 51.5 P < 0.001	G = 34.1 P < 0.001	G = 30.1 P < 0.001
III Aves Island, Venezuela			—	G = 0.1 NS	G = 32.3 P < 0.001	G = 22.4 P < 0.001	G = 19.9 P < 0.001
IV Matapica, Suriname				—	G = 51.5 P < 0.001	G = 34.1 P < 0.001	G = 30.1 P < 0.001
V Ascension Is., UK				—	—	G = 0.2 NS	G = 46.6 P < 0.001
VI Atol das Rocas, Brazil						—	G = 38.5 P < 0.001
VII Pailoa, Guinea Bissau						—	G = 26.2 P < 0.001
VIII Lara, Cyprus							G = 23.3 P < 0.001
B. INDIAN AND PACIFIC OCEANS							
	I	II	III	IV	V	VI	
I Ras Al Hadd, Oman	—	G = 32.8 P < 0.001	G = 38.7 P < 0.001	G = 19.5 P < 0.001	G = 0 NS	G = 0 NS	
II Queensland, Australia		—	G = 33.2 P < 0.001	G = 40.8 P < 0.001	G = 19.5 P < 0.001	G = 21.6 P < 0.001	
III Ogasawara Is., Japan			—	G = 48.7 P < 0.001	G = 22.6 P < 0.001	G = 25.1 P < 0.001	
IV Hawaii, USA				—	G = 9.6 P < 0.005	G = 11.0 P < 0.001	
V Michoacan, Mexico					—	G = 0 NS	
VI Galápagos, Ecuador						—	

TABLE 4. N_m values from Slatkin's (1989) cladistic approach (below diagonal) and Takahata and Palumbi's (1985) G_{ST} estimator (above diagonal). The 95% confidence intervals for Slatkin's estimator are in parentheses.

A. ATLANTIC OCEAN AND MEDITERRANEAN SEA								
	I	II	III	IV	V	VI	VII	VIII
I Florida, USA	—	19.6	1.5	0.1	0.4	0.2	0.1	0.1
II Tortuguero, Costa Rica	0.4 (0–1.2)	—	1.3	0.0	0.3	0.1	0.0	0.0
III Aves Island, Venezuela	0.5 (0–2.4)	0.5 (0–2.4)	—	1.0	1.1	1.3	0.5	0.5
IV Matapica, Suriname	0.0 (0–0.3)	0.0 (0–0.3)	0.4 (0–1.2)	—	0.3	0.1	0.0	0.0
V Ascension Is., UK	0.0 (0–0.3)	0.0 (0–0.3)	0.0 (0–0.3)	0.0 (0–0.3)	—	1.3	0.3	0.3
VI Atol das Rocas, Brazil	0.0 (0–0.3)	0.0 (0–0.3)	0.0 (0–0.4)	0.0 (0–0.3)	0.4 (0–1.2)	—	0.1	0.1
VII Pailoa, Guinea Bissau	0.0 (0–0.3)	0.0 (0–0.3)	0.0 (0–0.4)	0.0 (0–0.3)	0.0 (0–0.3)	0.0 (0–0.3)	—	0.0
VIII Lara, Cyprus	0.0 (0–0.3)	0.0 (0–0.4)	0.0 (0–0.4)	0.0 (0–0.4)	0.0 (0–0.3)	0.0 (0–0.4)	0.0 (0–0.4)	—
B. INDIAN AND PACIFIC OCEANS								
	I	II	III	IV	V	VI		
I Ras al Hadd, Oman	—	0.0	0.7	0.3	High	High		
II Queensland, Australia	0.0 (0–0.3)	—	0.6	0.1	0.0	0.0		
III Ogasawara Is., Japan	0.0 (0–0.3)	0.4 (0–1.2)	—	0.6	0.7	0.7		
IV Hawaii, USA	0.4 (0–1.2)	0.0 (0–0.3)	0.0 (0–0.3)	—	0.3	0.3		
V Michoacan, Mexico	High	0.0 (0–0.4)	0.0 (0–0.4)	0.5 (0–2.4)	—	High		
VI Galápagos, Ecuador	High	0.0 (0–0.4)	0.0 (0–0.4)	0.5 (0–2.4)	High	—		

relative to many other assayed vertebrates (Wilson et al., 1985; Avise et al., 1987). If the Atlantic versus Pacific assemblages of green turtles have been isolated since the rise of the Isthmus of Panama some 3 million years ago (Lundelius, 1987), then net nucleotide divergence between the Atlantic and Pacific mtDNA lineages ($P = 0.006$, after correction for within-ocean divergence) is an order of magnitude lower than predicted under the "conventional" mtDNA clock calibration of 2% divergence per million years originally suggested for primates (Brown et al., 1979). However, a several-fold slower mtDNA rate (roughly 0.2 to 0.4% between lineages per million years) has been suggested for other marine, freshwater, and terrestrial turtles (order Testudines) (Bowen et al., 1991; Avise et al.,

1992). Under such clock calibrations, Atlantic and Pacific populations of *C. mydas* may have been isolated for 1.5 to 3 million years.

However, estimated times of lineage separation must be interpreted with caution, and we cannot rule out the possibility that Atlantic and Pacific turtles shared a common ancestor subsequent to formation of the Panama Isthmus. The Cape of Good Hope is not an impermeable barrier to tropical species (Briggs, 1974), and this route might have provided a more recent link between Atlantic and Indian-Pacific green turtle populations. The fact that South and East Atlantic genotypes ("F" and "G" in Fig. 3) are the closest Atlantic relatives to Indian-Pacific mtDNAs may be interpreted as support for this scenario. However, the

converse expectation, that an Indian Ocean genotype is the closest Indian-Pacific relative to Atlantic mtDNAs, is not met with our single Indian Ocean rookery sample ($N = 15$). The Indian-Pacific mtDNA lineages most closely related to those in the Atlantic ("K," "L," "M," and "N"—Fig. 3) are found in the central and west Pacific. This pattern could be construed as evidence that the most recent contact between Atlantic and Indian-Pacific populations was through the east Pacific rather than from the Indian Ocean via the Cape of Good Hope. While this issue remains unresolved, we note that the Indian Ocean was not well sampled in this survey. It is possible that samples from other major Indian Ocean rookeries could resolve this question.

Intraoceanic Distribution of mtDNA Lineages

Green turtle nesting populations within ocean basins also exhibit significant geographic structure with respect to mtDNA genotype frequencies (Table 3), although the magnitudes of estimated sequence divergence among the haplotypes involved are considerably lower than those between the Atlantic-Mediterranean and Indian-Pacific Oceans (Fig. 2). With the exception of one individual from Brazil (genotype "F"—Fig. 3), no observed Atlantic genotype is more than three assayed restriction site changes removed from any other in the Atlantic. The shallow separation of Atlantic mtDNA lineages suggests that no physical impediments to green turtle dispersal have existed in the tropical Atlantic during recent evolutionary history. This interpretation is consistent with the known geologic history of the Atlantic Ocean basin.

The shallow evolutionary depth in the mtDNA phylogeny also suggests that the particular phylogeographic structure of female lineages within the Atlantic-Mediterranean realm is probably transient over evolutionary time spans. Carr and Coleman (1974) proposed an ancient (70 mya) origin for the Ascension Island green turtle nesting colony, based on a hypothesized colonization event of a proto-Ascension Island soon after the Cretaceous opening of the South Atlantic by plate tectonic movement. The mtDNA data are consistent with the iso-

lation of Ascension Island from most other Atlantic rookeries, but over a vastly shorter time scale (Bowen et al., 1989). With the addition of data from more rookeries in the current study, it appears that the closest maternal relatives of Ascension Island turtles occur in the geographically proximate Brazilian site, the only other locale where the mtDNA haplotype that is nearly fixed on Ascension Island ("D", Table 2) was observed.

Overall, we interpret the shallow separations in the entire Atlantic-Mediterranean mtDNA phylogeny to indicate that female breeding assemblages have been connected relatively recently in evolutionary time, probably through processes of rookery extinction and colonization. Climatic and geologic events (e.g., hurricanes, sea level changes) no doubt create and destroy green turtle nesting habitat, and thereby influence rookery turnover, with net effect that all turtles within the Atlantic-Mediterranean share a common ancestor more recently than would have been the case under longstanding rookery isolations. Based on the mtDNA clock calibrations for Testudines suggested above (0.2 to 0.4% sequence divergence per million years), all breeding populations within the Atlantic appear to have shared a common ancestor within the last 0.5 to 1.0 million years.

The Indian-Pacific Ocean mtDNA phylogeny has somewhat deeper mtDNA branches (Fig. 2). Genetic distances between haplotypes range from $P = 0.0008$ to 0.0044 (as compared to Atlantic-Mediterranean distances of $P = 0.0008$ to 0.0034 , or of $P = 0.0008$ to 0.0027 if we exclude the one individual with genotype "F"). Several factors may have contributed to this pattern. First, fewer localities were sampled from a much wider area. Second, the deeper nodes may reflect a larger total population size for green turtles in this oceanic basin (see Avice et al., 1988). Another influence may involve the geography of the shallow Indo-Pacific continental shelf. The Torres Strait, which separates Australia from Papua New Guinea, was exposed repeatedly during periods of lower sea level associated with Pleistocene glacial epochs (Doutch, 1972). In these circumstances, Australia and Papua New Guinea constituted a continuous land bar-

rier across tropical and temperate zones of the south Pacific. Partial barriers also may have existed between Indonesia and southeast Asia during glacial maxima. Thus gene flow across the Indo-Pacific may have been restricted or curtailed intermittently. Another possible factor involves habitat availability. The Pacific Basin includes broad stretches of open ocean "desert" in which adult green turtle habitats (both feeding and nesting) are absent. For example, the east Pacific is widely recognized as a formidable zoogeographic barrier for nonpelagic organisms (Briggs, 1974). Thus, the patchy distribution of green turtle habitat in the Indian and Pacific Oceans may contribute to deeper phylogenetic separations than observed in the Atlantic.

On the other hand, recent connection among Indian and Pacific rookeries is also indicated, as judged by the widespread distribution of haplotypes "I" and "L" (Table 2; Fig. 2). Curiously, "I" was shared by rookeries in the East Pacific, Central Pacific, and Indian Oceans, but absent in our collections from the Western Pacific. Based on the distribution of this mtDNA genotype, Indian Ocean and East Pacific lineages may be more closely related to each other than to the spatially intermediate rookeries in Australia and Japan.

Systematics of the Chelonia mydas Complex

The behaviors and morphologies of green turtles vary geographically. With respect to behavior, nesting seasons differ widely in timing and duration, even among rookeries in the same region (Pritchard, 1980). Some locales support both nesting and feeding aggregates, and nonmigratory populations may exist at these sites (Pritchard, 1971; Carr, 1980; but see Limpus et al., 1992). With respect to morphology, South Atlantic nesters are notably larger than Caribbean nesters (Carr and Goodman, 1970), which in turn are larger than those in the East Pacific (Pritchard, 1979; Figueroa, 1989) and Mediterranean. From these and related considerations, subspecific status has been proposed for numerous regional forms of the green turtle, including populations in the Caribbean (*C. m. viridis*), South Atlantic (*C. m. mydas*), Indo-west Pacific (*C. m. japon-*

ica), Gulf of California (*C. m. carrinegra*), and East Pacific (*C. m. agassizi*) (reviews in Carr, 1975; Pritchard and Trebbau, 1984; Groombridge and Luxmoore, 1989).

The east Pacific form is often accorded full species status: *C. agassizi*, the black turtle. These turtles tend to be distinguishable by carapace shape, small size, and dark coloration (Figueroa and Alvarado, 1990; Alvarado and Figueroa, 1990). However, light colored *C. mydas*-type individuals also nest at major East Pacific rookeries (Carr, 1961; Pritchard, 1971).

The divergence of Atlantic-Mediterranean and Indian-Pacific mtDNA genotypes (Figs. 2 and 3) is compatible with geographic considerations for *C. mydas*, but conflicts with the widely accepted taxonomic distinction for *C. m. agassizi*. Similar conflicts, in which molecular partitions are concordant with zoogeographic boundaries but not with taxonomic boundaries, have been noted in other recent studies (Avice, 1989; Meyer et al., 1990). Although we cannot exclude the possibility of undetected mtDNA phylads in putative *C. m. agassizi* populations, such lineages would have to occur at rather low frequency in the Galápagos ($N = 8$) and Michoacan, Mexico ($N = 7$) to have escaped detection in this survey. Notably, these locations represent two of the major *C. m. agassizi* rookeries.

Although mtDNA data do not support the evolutionary distinctiveness of *C. m. agassizi*, any taxonomic determination should rest on multiple lines of evidence. In the case of ridley sea turtles (*Lepidochelys* spp.), conclusions drawn from morphology and mtDNA data independently corroborate the evolutionary distinctiveness of *L. kempi* from *L. olivacea* (Bowen et al., 1991). Thus additional lines of evidence, including those from nuclear gene assays (Hendrickson, 1979, 1980; Karl et al., 1992), are desirable before final conclusions on *C. m. agassizi* are drawn. If the global pattern observed in the mtDNA phylogeny is corroborated with other evidence, then the *Chelonia* complex should probably be divided into Atlantic-Mediterranean and Indian-Pacific subspecies, with additional population-level differentiation recognized within each ocean basin. Under this scenario, the Indian-Pacific green turtle subspecies should

cliffs predominate above and below the water line. The sea-level drop associated with the Wisconsin glacial interval (estimated at 100 meters—Bowen, 1978) may have precluded nesting here as well. In addition to sea level changes, global cooling associated with Pleistocene glacial advances no doubt reduced the northern and southern limits of green turtle nesting. Hedgpeth (1954) demonstrated that the temperate Atlantic fauna extended well south of the Florida peninsula during the Wisconsin glaciation, and cool temperate conditions also extended into the eastern Mediterranean (Buckley et al., 1982). Thus the sites of present-day rookeries in Florida and Cyprus were probably too cool to support nesting even 10,000 years ago.

Feeding grounds may be transient as well. The continental shelf of Brazil, which currently supports one of the largest green turtle feeding grounds in the Atlantic, ends less than 100 meters below current sea level (Moll, 1983). Thus at times of lower sea level these feeding grounds were probably displaced or highly compressed.

Given the brief duration of rookeries over geologic timescales, absolute natal homing would be a recipe for extinction. As climatic fluctuations alter the availability of green turtle habitat, new nesting beaches and feeding grounds must be colonized by turtles hatched elsewhere. As noted by Carr et al. (1978), "Strays and wandering must occur, and are no doubt adaptively advantageous aberrations, necessary for colony proliferation . . ." In the cases noted above, green turtle feeding and nesting habitats probably have been colonized within the last 500 green turtle generations. Thus, the shallow population structure observed within ocean basins is probably understandable in terms of the temporal lifespans of green turtle habitat.

Considering the ephemeral nature of rookeries, it is perhaps surprising that detectable genetic structure exists. Under neutrality theory, mtDNA gene trees are expected to be concordant with population structure only after about $2N_{fe}$ generations of population isolation (Neigel and Avise, 1986; Pamilo and Nei, 1988), where N_{fe} is the evolutionary effective population size of females. One consequence of this lineage sorting process is that a longer generation

length is expected to increase the chronological time required for gene lineages within an ancestral population to resolve into distinct genetic lineages in isolated daughter populations (Bowen and Avise, 1990). Any analysis of green turtle population genetic processes must weigh the consideration that green turtle generations are an order of magnitude longer than those of most vertebrates. If we conservatively assume a generation length of 20 years, and an N_{fe} of 1,000 per rookery, then green turtle populations would require 40,000 years on average to evolve fixed lineage differences (as observed between Ascension and Suriname). Organisms with longer generation lengths or larger populations would require greater times to attain reciprocal monophyly. These time intervals are probably considerably longer than the evolutionary life span of most rookeries.

Why then are green turtle female lineages geographically structured under these ephemeral conditions? One possibility is that new nesting beaches may be colonized by only one or a few gravid females, leading to rapid fixation of a mtDNA genotype in the neophyte rookery. The low nucleotide diversity within most surveyed rookeries may be construed as evidence supporting this possibility. In our assays, most rookeries (12 of 15) exhibited only one mtDNA haplotype or two haplotypes that differed by a single restriction site change (Table 2). Only the Japanese and Polynesian samples contain divergent genotypes that necessitate a hypothesis of multiple colonization events.

Management Implications

Natal homing on a regional or rookery-specific basis appears to be a dominant force shaping female green turtle population structure. However, a low level of leakage presumably exists that enables exploitation of new habitat. What role do "gravid waifs" have in the demography and hence management of rookery populations? Colonization events probably occur on a time scale of thousands of years. While this is an important evolutionary consideration, estimates of migration (Table 4) indicate that gene flow between rookeries is too low to significantly impact recruitment on a contemporary scale. In terms of conservation

and management, mtDNA data indicate that rookeries must be considered independent demographically. It is notable that rookeries extirpated over the last four centuries (including Grand Cayman, Bermuda, and Alto Velo) have not been recolonized by natural recruitment (Parsons, 1962). Thus both historical records and current genetic evidence indicate that overharvesting of nesting assemblages is not compensated by recruitment from other rookeries. Because the production of progeny ultimately depends on female nesting success, the conclusion that rookeries must be managed independently holds even if males should prove not to be philopatric to natal site.

Prospectus

The current study has addressed only the matrilineal component of population structure and natural history in *C. mydas*. The biology of this species is such that matriarchal pedigrees are of special relevance to the issues of demographic independence of rookeries and natal homing by green turtles. Many questions that remain about the natural history of green turtles involve male behaviors. Because males seldom come ashore where they might otherwise be observed and tagged (but see Balazs, 1983), little is known concerning their dispersal and migratory behavior, the mating system, or whether males provide a significant avenue of gene flow between some of the rookeries that we now know to be nearly completely isolated with respect to female lineages. In a companion report, we empirically address these issues from the perspective of nuclear gene analyses (Karl et al., 1992).

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Abstract. – Female yellowtail rockfish *Sebastes flavidus*, a viviparous species employing intraluminal gestation following fertilization of ovulated eggs, were caught from Cordell Bank (seamount 20 miles west of Pt. Reyes, central California) on a monthly basis from May 1985 through April 1986 to determine their annual reproductive cycle. Since histological methods provide precise and detailed information, this method was employed to (1) examine oocytes and embryos to describe developmental stages, and (2) provide temporal assessment of the annual reproductive cycle. The description and staging scheme developed provide a basis to compare reproductive developmental patterns between cycles and populations.

Oogonia (Stage I) and early perinucleolus (Stage II) oocytes were present in samples from all months. Progressive growth of oocytes from early- to late perinucleolus (Stage III) was evident in spent and recovering ovaries, indicating the end of a reproductive year and the beginning of a new reproductive cycle. Initial yolk accumulation (Stage IV) occurred in July, and final yolk accumulation (Stage V) was predominant from September through January. In February, the majority of samples displayed fertilized ova in early-celled stages of embryonic development. Gestation continued for about 30 days with parturition occurring between January and March. Mature oocytes were also collected in March, suggesting the Cordell Bank yellowtail population has a prolonged reproductive season extending into April.

Annual reproductive cycle of oocytes and embryos of yellowtail rockfish *Sebastes flavidus* (Family Scorpaenidae)

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Sixty species of rockfish (genus *Sebastes*) have been recorded in waters off the California coast; twenty species are utilized by commercial and recreational fisheries (Lenarz 1986). Rockfishes display a wide variety of life history patterns with respect to their habitat and seasonality of reproduction (Wyllie Echeverria 1987). The majority of investigations on rockfish reproduction have focused on the development, occurrence, and identification of larvae and juveniles. Evaluating annual reproductive success as a direct consequence of variations in oocyte viability has received less attention.

The *Sebastes* complex contributed approximately 37,806 mt to west coast fisheries in 1985 (PFMC 1990) and management of this resource is heavily dependent upon predictions of strong and weak year-classes. Since no single trait accurately represents reproductive capacities of fish populations (Eldridge et al. 1991), fisheries management is based on a variety of information. Year-class strength estimates may be enhanced by understanding factors influencing annual fluctuations in reproduction. Reproduction within this genus is characterized by intraluminal gestation, following fertilization of ovulated, mature eggs. This process is somewhat unique among teleosts occurring only in scorpaenids and zoarcids (Wourms et al. 1988). The investigation described here

focuses on the development and temporal occurrence of oocytes and embryos within the ovary of yellowtail rockfish *Sebastes flavidus*. Characterization of oocyte growth and embryonic development provides a basis for assessing reproductive performance. This study is part of a larger effort to acquire information on the reproductive biology of yellowtail rockfish to ultimately determine factors that influence reproductive success.

Although characteristics of oocyte growth are generally similar among teleosts (Wallace and Selman 1981), numerous ovary maturity scales and oocyte classification schemes exist (Yamamoto 1956, Htun-Han 1978, Robb 1982, Howell 1983). These classification schemes are useful for determining reproductive strategies (synchronous, group-synchronous, or asynchronous) and evaluating aspects of reproductive trends. Each oocyte staging system is, however, less likely to be adapted for teleosts outside the genus of original study due to the variety of reproductive strategies. An oocyte classification scheme to assess the reproductive status of the marine, viviparous genus *Sebastes* in the Eastern Pacific has not been reported. Taking these factors under consideration, the objectives of the study reported here were two-fold: (1) to describe oocyte and embryonic development in *Sebastes flavidus* through one complete reproductive cycle, and (2) establish a staging

classification as a basis for the comparison of oocyte and embryonic development between populations, reproductive years, and other species of *Sebastes*. Such data may be used to monitor reproductive development during a particular year. In addition, descriptions of oocyte and embryonic development provide a basis to compare the impacts of environmental fluctuations and physiological responses with the production of viable offspring. An understanding of environmental and physiological interactions influencing reproductive success could provide valuable contributions to the understanding of recruitment dynamics and allow for more efficient resource management.

Materials and methods

Specimens were collected from Cordell Bank (38°00'N, 123°25'W), a seamount 20 miles west of Pt. Reyes, at monthly intervals. Adult female yellowtail rockfish were captured by hook-and-line at depths of 50–150 m, from May 1985 through April 1986. No samples were obtained in June 1985 due to inclement weather. Mean age and size of samples for each month are shown in Table 1.

Fish were held on ice and transported to the laboratory where pieces of ovaries (~4 × 4 × 6 mm) were dissected and fixed in 10% neutral buffered formalin. Routine paraffin embedding followed the guidelines of Humason (1967). Samples were sectioned at 6 μ thickness with a rotary microtome. Mounted sections were stained in hematoxylin and counterstained in eosin (H&E).

Cell measurements were made using a video coordinate digitizer (Model 582 AVCD, H.E. Inc., Las Vegas, NV) on cells sectioned through the nucleus. Oocytes were measured and staged randomly. Mean cell diameters were determined from a subsample of 10–20 cells for each stage. All cell diameters reported are from fixed tissues.

In each monthly sample, the first 200–400 cells encountered were counted and staged. Percent frequency distributions of the various oocyte stages were calculated by dividing the total number of a particular stage by the total number of oocytes observed, expressed as a percentage. Because the probability of an individual oocyte being sectioned is proportional to its size as well as its abundance, larger oocytes tend to be overestimated and smaller oocytes underestimated (Howell 1983). Nonetheless, frequency distributions do indicate seasonal changes within the ovary. Because of the wide range of cell diameters, overlapping sizes among oocyte stages, and shrinkage due to fixation, criteria for staging oocytes was based on histological appearances and cell structure.

Table 1

Monthly means and standard errors for age, standard length (SL), and weight (Wt) of *Sebastes flavidus* collected off central California, May 1985–April 1986, used for histological analysis.

Month	Age (yr)	SL (cm)	Wt (g)	n
May	14.7 ± 2.0	37.4 ± 1.0	1434 ± 115	6
June	—	—	—	0
July	17.9 ± 2.3	39.5 ± 1.5	1600 ± 146	9
Aug.	13.2 ± 2.0	36.8 ± 1.8	1387 ± 181	4
Sept.	30.0 ± 2.6	44.4 ± 0.6	2349 ± 111	6
Oct.	26.2 ± 4.0	42.6 ± 1.2	2017 ± 157	7
Nov.	21.1 ± 2.2	40.9 ± 0.6	1780 ± 97	6
Dec.	18.7 ± 2.1	39.3 ± 1.1	1830 ± 122	10
Jan.	15.4 ± 1.8	36.1 ± 1.1	1272 ± 107	10
Feb.	14.6 ± 1.8	36.1 ± 1.1	1315 ± 83	10
Mar.	19.3 ± 1.8	37.5 ± 1.2	1489 ± 102	10
Apr.	23.4 ± 2.2	38.3 ± 0.6	1387 ± 52	10

Although ovaries in varying stages of postfertilization development were observed, monthly collection of ovaries was inadequate for a detailed study of rapid embryonic development. Therefore, additional samples of embryonic stages were collected by catheterization from female yellowtail rockfish captured after copulation from female yellowtail rockfish captured after copulation were catheterized weekly for 6 weeks while being maintained in a flow-through, sand-filtered (to 10 μ) seawater system. Photoperiod was ambient. The mean temperature and salinity (10.4 °C and 34.7‰) for the 2-month holding period (January and February) were well within the range of parameters at the sampling site.

Abbreviations used in figures

BC	blastodermal cap	MU	muscle
BR	brain	NC	notochord
C	capillary	NU	nucleoli
CH	chorion	N	nucleus
EB	embryonic body	OG	oil globule
EF	empty follicle	ON	oogonial nest
ER	erythrocyte	OP	optic vesicle
EY	eye	OV	oil vacuole
FOL	follicle	POF	postovulatory follicle
G	granulosa	RE	retina
GR	germ ring	SO	somite
HG	hind gut	T	theca
LC	lamprush chromosome	VM	vitelline membrane
LN	lens	YG	yolk globule
LT	liver tissue	YM	yolk mass
MN	migratory nucleus		

Table 2

Classification and temporal occurrence of oocytes from *Sebastes flavidus* collected off central California, based on histological appearance. See text for additional histological descriptions.

Stage	Major histological characteristics	Temporal occurrence
I Oogonia	Small cells (5–25 μ) found in clumps or "nests." Cytoplasm pale to clear. Basophilic nucleus occupying most of cell volume.	All year
II Early perinucleolus	Wide range of cell diameters (20–100 μ). Intense basophilic cytoplasm. One or two large nucleoli in nucleus.	All year
III Late perinucleolus	Diameters 50–140 μ . Small, clear vesicles present in cytoplasm. Cytoplasm pale-blue to light-gray. Several small nucleoli around inner margins of nuclear membrane.	Feb.–Oct.
IV Initial yolk accumulation	Cell diameters 120–210 μ . Small spherical, eosinophilic yolk granules in a distinct cortical zone in cytoplasm. Cytoplasm vesicular and light-gray. Well-developed follicle surrounds a developing vitelline membrane. Several small nucleoli around the inner margins of nuclear membrane.	July–Oct.
V Final yolk accumulation	Large cells (200–600 μ). Cell volume one-half to entirely full of yolk spheres. Lampbrush chromosomes visible in nucleoplasm. Lipid vacuoles appear larger as they coalesce.	Sept.–March
VI Migratory nucleus	Cell diameters 600–750 μ . A single, large lipid vacuole present. Nuclear membrane indistinct or absent. Nuclear material irregularly shaped and no longer centrally located. Follicle may be distorted and irregularly shaped.	Dec.–March
VII Ovulation & Fertilization	Mature oocyte free from follicle. The yolk mass is a single, large homogeneous mass, staining deep-purple. In fresh (unfixed) ovaries, ova appear clear or translucent.	Dec.–March

Results

Oocyte development

Major histological characteristics distinguishing stages for *S. flavidus* are listed in Table 2. All cells could be categorized into one of the seven stages. Terminology and nomenclature follow Moser (1967a) and Howell (1983).

Stage I: Oogonia These small cells were 5–25 μ in diameter and were found in clumps or "nests" along the lamellar branches (Figs. 1A, 4E). Larger oogonia in the 20 μ range possessed a deeply-stained chromatin network attached to a single, large basophilic nucleolus.

Stage II: Early perinucleolus These oocytes were 20–100 μ in cell diameter. While still closely associated with neighboring oogonia, there was noticeable movement away from oogonal nests. The most obvious feature of this cell was the intensely basophilic cytoplasm (Figs. 1B, 4E).

Stage III: Late perinucleolus Diameters were 50–140 μ . Clear vacuoles appeared in the cytoplasm of oocytes as small as 50 μ . Initially these vacuoles were distributed as a poorly organized ring surrounding the

nucleus, but were seen randomly scattered throughout the cytoplasm of larger oocytes (Figs. 1B, 4E). As growth continued, they increased in size and number.

Stage IV: Initial yolk accumulation The earliest signs of yolk accumulation were seen in oocytes of 120–210 μ in diameter. Small, spherical globules of yolk were seen in a distinct cortical zone in the cytoplasm (Fig. 1C,D). The follicle enclosing the oocyte is more complex and composed of several identifiable structures (see below).

Stage V: Final yolk accumulation To simplify the staging of yolked oocytes, cells with approximately one-half their volume filled with yolk spheres, and cells whose volumes were entirely filled with yolk, were placed in Stage V. Yolk spheres increased in number and size. By the end of this stage, the cell diameter increased to about 650 μ . The cytoplasm was entirely filled with yolk spheres of various sizes (Fig. 2A). The vacuoles which were distributed throughout the cytoplasm began to coalesce, forming larger vacuoles.

An eosinophilic nucleoplasm with lampbrush chromosomes was visible (Fig. 2B). In the late Stage-V cell, the nucleus became irregularly shaped and the nuclear membrane was often indistinct (Fig. 2A).

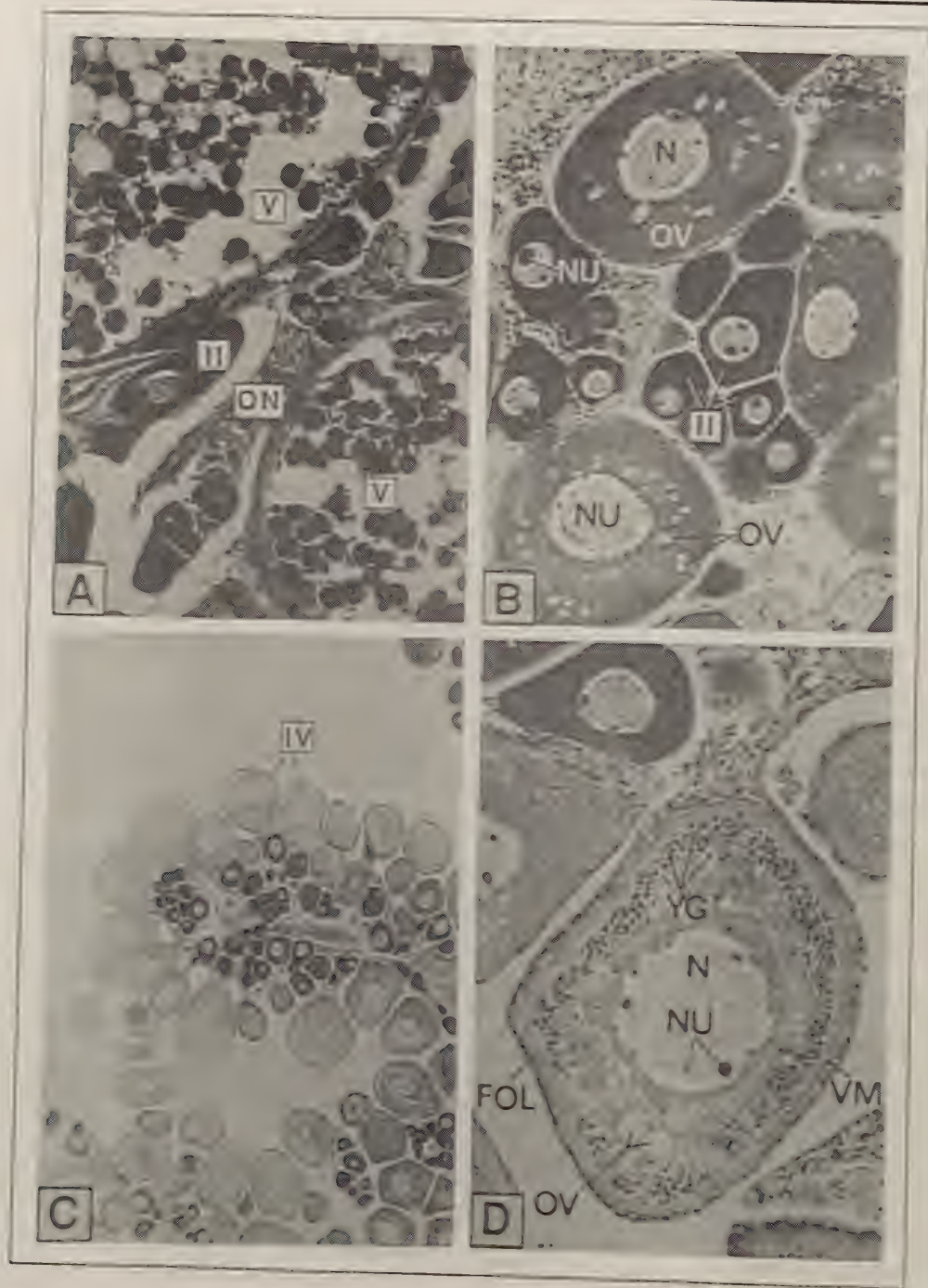


Figure 1 (left page)

(A) Oogonial nest (Stage-I oocyte) from *Sebastes flavidus*, containing several primary oocytes collected Dec. 1985, 400 $\times$. (B) Section of oocytes in ovary of *S. flavidus* collected May 1985, 250 $\times$. Basophilic properties of cytoplasm in Stage-II cells and their large nucleoli are shown. Distribution of vacuoles are seen in the larger Stage-III cells. (C) Cross-section of an ovary collected Aug. 1985 showing arrangement of Stage-IV oocytes in grape-like clusters on outer margins of a lamellar branch, 63 $\times$. (D) Typical Stage-IV (initial yolk accumulation) oocyte showing the first indications of yolk, 250 $\times$.

The cellular composition of the mature follicle was best observed in Stage-IV or Stage-V oocytes (Fig. 2D). A bilaminar vitelline membrane about 1 μ in thickness was next to the plasma membrane of the oocyte. Outside the vitelline membrane was a single inner epithelial layer, the granulosa. Encapsulating the granulosa was an intricate capillary network filled with erythrocytes. The theca, a single epithelial layer consisting of squamous cells with large nuclei, surrounded the profuse capillary system.

Stage VI: Migratory nucleus Cell diameters ranged from 600 to $\sim$ 750 μ . Lipid material had coalesced to form a single, large vacuole, usually centrally located. Nuclear material was ameboid in appearance and no longer occupied a centralized position in the cell (Fig. 2C). Nucleoli were small, indistinct, or entirely absent.

Stage VII: Ovulation/Fertilization Histological evidence of ovulation was verified by observing the integrity of the surrounding follicle. Follicles appeared either as irregularly shaped and shrunken away from the oocyte or displayed a loss of continuity. Postovulatory follicles appeared throughout the sectioned ovary (Fig. 2C).

Because fertilization of the mature oocyte occurs rapidly after ovulation, distinction between ovulated oocytes and recently-fertilized oocytes was unnecessary. Therefore, fertilization was considered an event rather than a stage of histological distinction, and is included in Stage VII to maintain logical continuity of the developmental process. Following fertilization, however, the yolk material became a single homogeneous mass staining bright-purple in histological preparations, appearing clear or translucent in unfixed samples (Fig. 3A, B). This distinguishes fertilized from recently ovulated ova.

Embryonic development

A complete series of sequential embryonic developmental stages was not obtained from field collections due to the sampling interval and rapid development of

embryos. Embryos from field collections were, however, satisfactorily placed into one of three broad categories: (1) early-celled, (2) embryonic body, or (3) eyed-larvae (where retinal pigmentation was visible).

Early-celled The early celled stage of embryonic development observed from field collections of yellow-tail rockfish ovaries corresponded to stage 9 of Oppenheimer's classification for *Fundulus heteroclitus* (Oppenheimer 1937). The early-celled stage was seen as an undifferentiated mass of cells (blastodermal cap) on top of a large yolk mass (Fig. 3A). This stage was first collected in January, most frequently seen in February, and last occurred in March.

Embryos in a more advanced state (i.e., flattening or expansion of the blastula) occasionally occurred within an ovary primarily containing early-celled embryos. This suggests rapid cellular divisions and growth.

Embryonic body The appearance of an embryonic body was first seen in an ovary collected in February and last seen in March. This embryonic stage closely corresponds to Oppenheimer's stages 14 or 15 (Oppenheimer 1937). At the beginning of this stage, an undifferentiated mass of cells (taking on the appearance of tissue rather than individual cells) was located in a high ridge lying over the yolk mass. The oil globule was evident at the opposite pole (Fig. 3B). With further development, embryos displayed optic vesicles originating from lateral buds, distinguishing the cephalic region (Fig. 3C). By the end of this growth phase, somites along the trunk were visible along with lengthening of the tail. The head had further developed to include lens formation (Fig. 3D).

Figure 2 (overleaf, left page)

(A) Cross-section of ovary from *Sebastes flavidus* with clutch of oocytes in late Stage V, 63 $\times$. (B) Cross-section through nucleus of a Stage-V oocyte showing distribution of nucleoli and lampbrush chromosomes in the nucleoplasm, 400 $\times$. (C) Section through two nearly-mature oocytes in Stage VI (migratory nucleus), 63 $\times$. (D) Tangential section of Stage-V oocyte showing components of the follicle outside of vitelline membrane, 400 $\times$.

Figure 3 (overleaf, right page)

(A) Early-celled embryos from *Sebastes flavidus* ovary collected Feb. 1986, 63 $\times$. (B) First appearance of embryonic body, showing cellular differentiation. Whole embryo, formalin-fixed, 40 $\times$. (C) Section through developing embryo (embryonic body, late stage) showing optic vesicle formation originating from lateral expansions in cephalic region, 63 $\times$. (D) Embryonic body stage further developed than in Fig. 3C, with better definition of brain, retina, and lens formation, 63 $\times$.

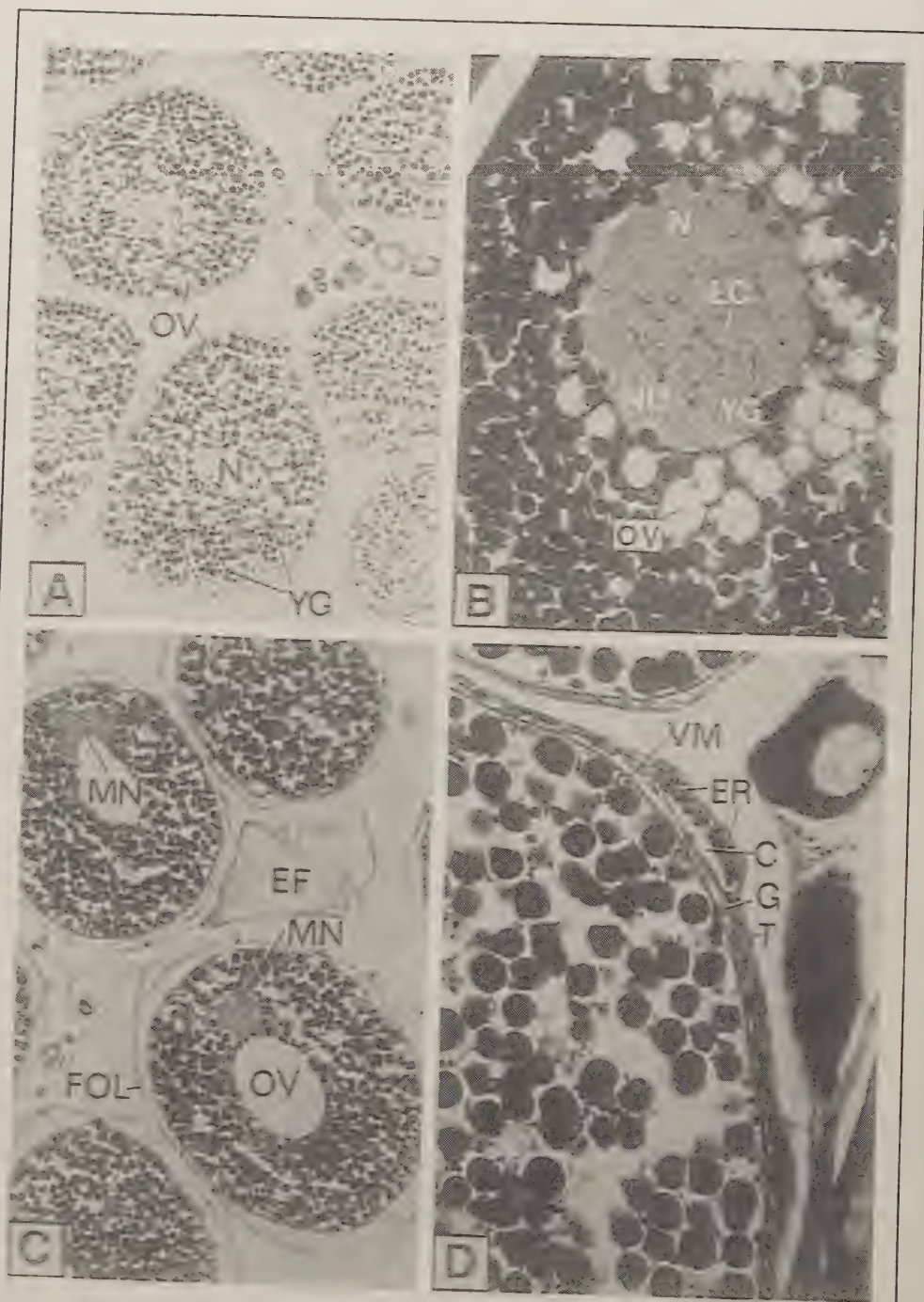


Figure 2

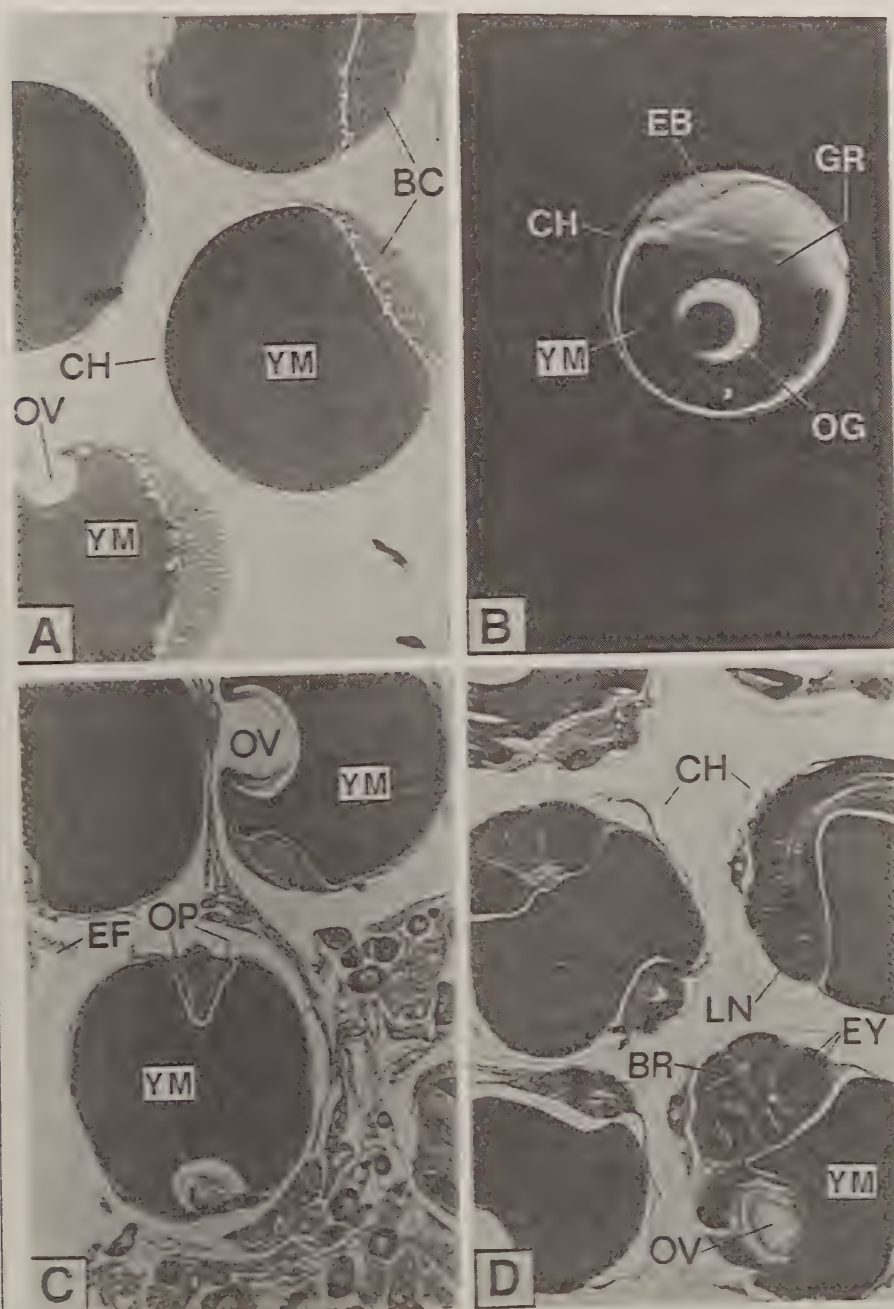


Figure 3

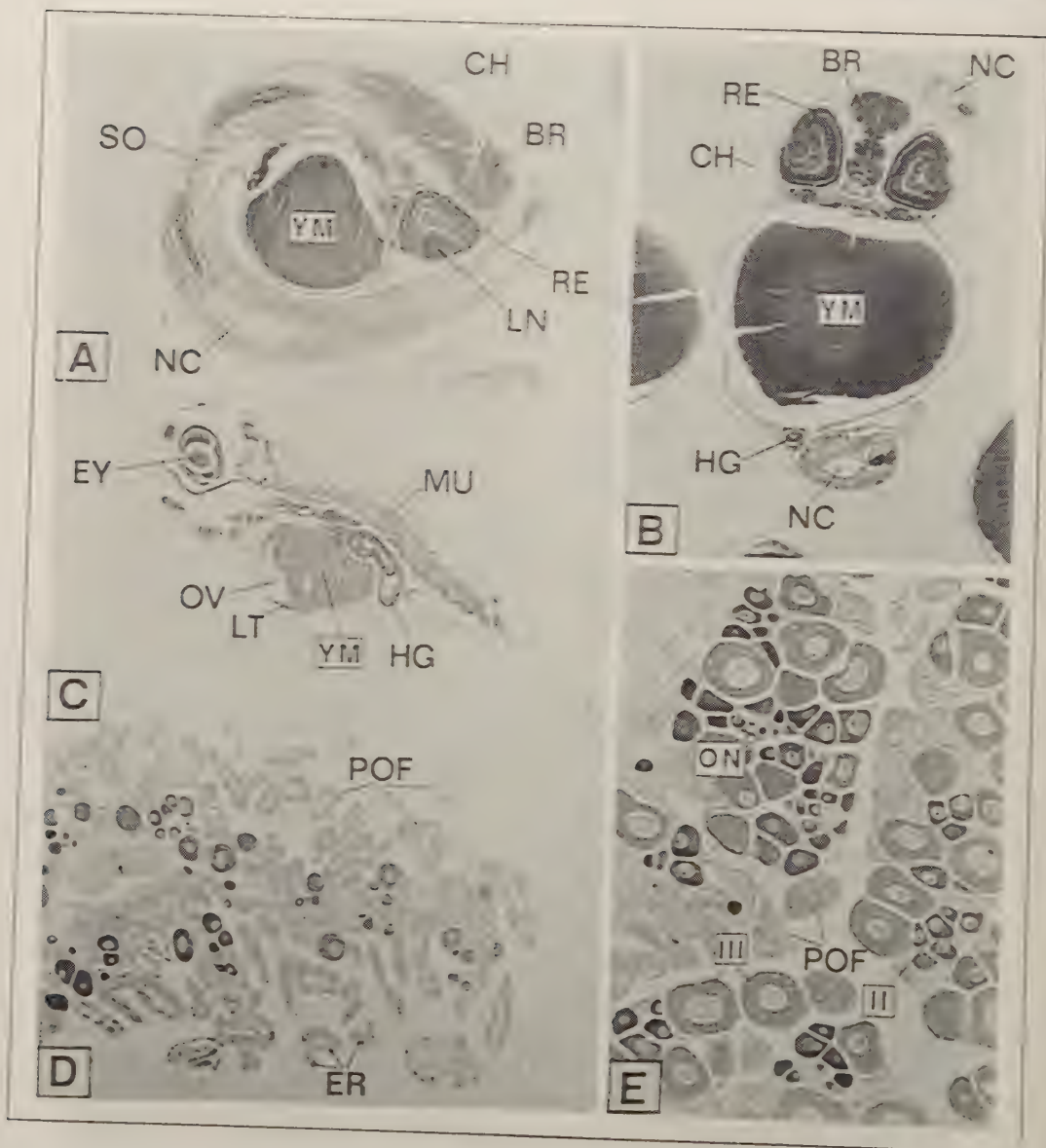


Figure 4 (above)

(A) Unhatched prolarvae of *Sebastes flavidus* collected Feb. 1986. Pigmentation of retina is apparent, as are well-formed somites, 63 $\times$. (B) Tangential section of unhatched prolarvae with completed pigmentation of the retina. Tail continues to lengthen and is seen to pass the head slightly, 63 $\times$. (C) Newly-hatched larva of *S. flavidus* showing close association of liver with oil vacuole, developing jaw and well-developed gut, 40 $\times$. (D) Cross-section of a recently-spent ovary of *S. flavidus* collected March 1986. Many empty and collapsed follicles are being resorbed, 40 $\times$. (E) Recovering and early developing ovary collected April 1986 showing reorganization of ovarian stroma as resorption nears completion, 63 $\times$.

Eyed-larvae Retinal pigmentation began as a black deposit outlining the periphery of the retina. Concurrently, somites were well formed in the thoracic and tail regions (Fig. 4A). Mature embryos (prehatching larvae) exhibited complete pigmentation of the eyes and a well-developed musculature system along the entire length of the tail (Fig. 4B). Embryos in this broad developmental category were in field samples collected in January and February. Had ovaries containing

hatched embryos (larvae) been collected in the field, they would have been included in this stage. Larvae were, however, taken from females held in the laboratory. These larvae were 4–6 mm in length and had open mouths with functional jaws. The yolk mass appeared to be reduced, and liver tissue was associated with a persistent oil globule (Fig. 4C).

Seasonal oocyte cycle Oogonial nests were observed in all samples, with about 25% frequency of occurrence throughout the entire reproductive cycle (Fig. 5). These Stage-I cells were most conspicuous early in the reproductive season and in ovaries of spent females.

Stage II or early-perinucleolus oocytes were also noted year-round and accounted for about one-third of all oocyte types observed (Fig. 5). The large nucleoli and dark cytoplasm were features that easily distinguish this stage. Mid- to late Stage-II cells were observed either singly or in groups around oocytes of later maturational stages (Stages III–VII) and were considered the 'resting' stage oocytes of other investigators (Bowers and Holliday 1961, Howell 1983).

In early spring, a broader range of Stage-II cell diameters was evident, indicating continued oocyte growth. Stage-III cells rapidly increased during March and April to a maximum frequency of 40% in April, and decreased in frequency by August as this clutch of oocytes developed (Fig. 5).

Copulation of yellowtail rockfish typically occurs over three months beginning in August and ending in October (Eldridge et al. 1991). The incidence and frequency of sperm in yellowtail rockfish ovaries were not evaluated in this study. However, small clumps or 'packages' of sperm were occasionally seen closely associated with the stroma or in spaces between developing (yolked) oocytes.

Initial yolk accumulation (Stage IV) was first documented in females collected in July, with all specimens collected in August showing this stage. In August, 34% of oocytes were Stage IV. Oocytes of Stage IV appeared as grape-like clusters on the outer margins of the lamellar branches, developing in a group-synchronous manner (Fig. 1C). The occurrence of Stage-IV oocytes sharply declined from August to November when no Stage-IV oocytes were observed (Fig. 5). As yolk accumulation continued, yolk spheres increased in size and number, filling the cytoplasm to about one-half its volume. At this point, oocytes were categorized as Stage V. Stage V was the most advanced oocyte observed from its first appearance in September until December when the frequency declined (Fig. 5). Oocytes in this developmental stage were most prevalent in November when they accounted for a mean of 48% of all oocytes. Stage-VI (Migratory nucleus) oocytes were first observed in December.

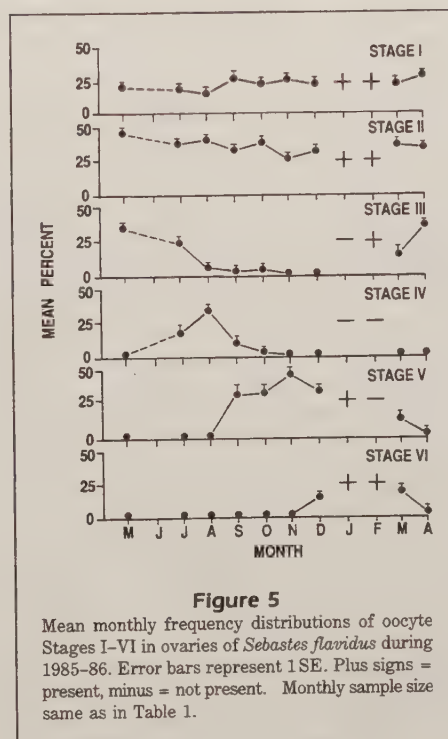


Figure 5
Mean monthly frequency distributions of oocyte Stages I–VI in ovaries of *Sebastes flavidus* during 1985–86. Error bars represent 1 SE. Plus signs = present, minus = not present. Monthly sample size same as in Table 1.

Ovaries with an advanced mode of Stage-VI oocytes continued to be collected over the next 3 months (January–March). This stage appeared to have a short duration, as ovaries containing Stage VII were also collected in some of the same months as Stage VI (December–February).

Ovary maturation was determined by using the most advanced oocyte or embryonic stage present in each monthly sample, and their frequency of occurrence was expressed as percent(s) (Fig. 6). Temporal ovarian development is illustrated and reflects a prolonged reproductive season.

While accurate frequency distributions on Stage-VII oocytes were not possible, the peak month of ovulation and fertilization appeared to be February. Sections of samples with Stage-VII oocytes showed eggs free from (e.g., outside) their follicular remnants. While continuity of follicular components (theca and granulosa) was disrupted, the integrity of the capillary network was maintained and there was a close association with the developing embryo.

Ovaries recently spawned (parturition) were seen as early as January and most frequently collected in March (Fig. 6). The ovary was greatly reduced in size,

reddish-blue in color, and very soft in texture. Histologically, the spent ovary displayed increased vascularization, a thickening of the tunica, and post-ovulatory follicles undergoing various stages of resorption (Fig. 4D). In addition, larvae remaining after parturition and yolked oocytes not reaching maturity are frequently seen in various stages of resorption.

Late-recovering and early-developing ovaries possessed reorganized lamellar branches containing Stages I, II, and early Stage-III oocytes as resorption nears completion (Fig. 4E). All samples collected in April were in this condition (Fig. 6), which marked the end of one reproductive season and the beginning of the next reproductive cycle.

Discussion

In the present study, I established an oocyte/embryonic classification that allows rapid determination of a rockfish population's status in the annual reproductive cycle. The use of this staging system allows one to establish oocyte frequency distributions and categorize ovaries as to their seasonal development, both temporally and spatially. This information, in turn, not only permits interannual and interpopulational comparisons, but may help reveal variations related to environmental factors.

Developmental events that occur in the oocytes of *Sebastes flavidus* are similar to those described for other teleosts with group-synchronous development (see review by Wallace and Selman 1981). Embryogenesis and the basic reproductive patterns follow observations reported for other members of the genus *Sebastes* (Moser 1967a, Wyllie Echeverria 1987). Temporal occurrence of reproductive events and seasonal variations of these events differ within the genus (Wyllie Echeverria 1987).

In the present work, oocyte development in *S. flavidus* has been categorized by separating oocyte growth into seven distinct stages. Oogonia and early-perinucleolus stages (Stages I and II, respectively) are found in the ovaries throughout the year. These stages appear to grow continuously, develop asynchronously, and, particularly in Stage-II cells, display a wide

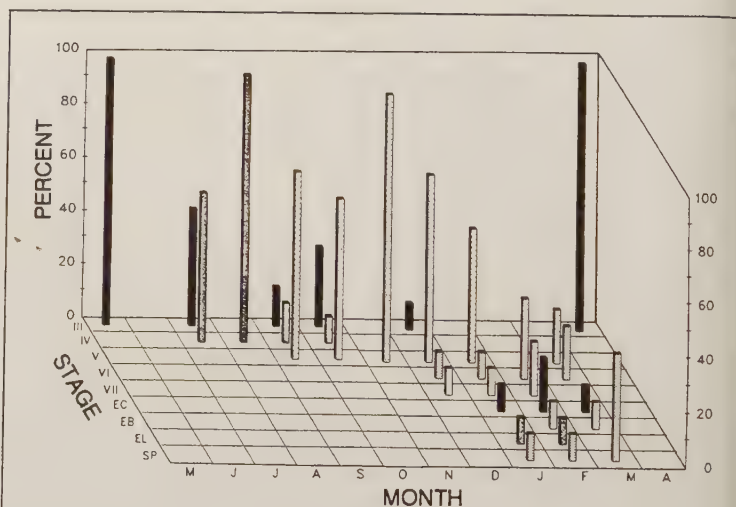


Figure 6

Percent distribution of ovarian maturation stages (derived from the most advanced oocyte or embryonic stage categorized histologically) from monthly collections of *Sebastes flavidus*; n is same as presented in Table 1. III = late perinucleolus, IV = early yolk, V = late yolk, VI = migratory nucleus, VII = ovulation/fertilization, EC = early-celled embryo, EB = embryonic body, EL = eyed-larvae, SP = spent.

range of cell diameters. Development of unyolked oocytes in *S. flavidus* is similar to that described for *S. paucispinus* (Moser 1967a,b). However, seasonal occurrence of Stage-III oocytes differs between the two species. Stage-III oocytes in *S. flavidus* decline rapidly in number as yolk accumulation (Stage IV) is initiated. They are not observed again in the ovaries until after parturition and the beginning of the reorganization of the lamellar branches. While Moser (1967a) did not suggest a staging classification scheme, his descriptions for *S. paucispinus* included oocytes corresponding to Stage III (in the present study). In contrast to *S. flavidus*, these oocytes occurred in ovaries of *S. paucispinus* throughout the year (Moser 1967a). The temporal difference in occurrence of Stage-III oocytes between these two species is most likely a reflection of the number of broods produced annually. Viviparous species producing more than one brood annually require a reserve of Stage-III oocytes. In rockfish where two or more broods of young are produced in one reproductive season, a second clutch of yolked oocytes develops concurrently with the initial brood of gestating embryos. Moser (1967a) reported the second clutch of yolked oocytes to occur in *S. paucispinus* when the initial brood had reached eye-lens formation. A distinct seasonal absence of Stage-III oocytes, or a

clutch of yolked oocytes during embryonic gestation, distinguishes single from multiple spawners.

There were approximately 30–40 days between the appearance of fertilized ova and well-developed larvae or recently-spawned females. Therefore, gestation appears to be 30–40 days in *S. flavidus*. Moser (1967b) estimated 1–2 months gestation for the multiple-spawner *S. paucispinus*, and Boehlert and Yoklavich (1984) noted 37 days for *S. melanops*, a single-season spawner. Similarly, Mizue (1959) compared a multiple-spawner, *S. marmoratus* to a single-season spawner, *S. inermis*. His data suggest approximately 30–45 days for embryonic gestation in both species.

While the basic reproductive pattern among the various *Sebastes* species is similar, variations exist in reproductive strategy and life history (Boehlert and Yoklavich 1984). Temporal variations in reproductive seasonality of rockfishes are perhaps the most obvious and, therefore, well documented. Releasing larvae over an extended period of time increases the probability that a portion of the reproductive population would encounter favorable environmental conditions for the survival of the progeny. Wyllie Echeverria (1987) listed the peak parturition months for 34 species of *Sebastes* and reported that larval extrusion occurs for up to 9 months in some species. In her study, from samples collected over a 7-year period, the principal month of parturition for yellowtail rockfish was February. In the present study, and in more recent work (unpubl. data), March was the peak month of parturition; however, the samples were from a smaller geographical area. Phillips (1964), who sampled northern, central, and southern California rockfish populations, determined *S. flavidus* to be a "winter" spawner (November–March). Wyllie Echeverria (1987) reported parturition for yellowtail rockfish from north-central California to occur from January to July. In the present study, a shorter parturition time was observed for the Cordell Bank yellowtail population (January–March). This temporal variance may reflect a clinal reproductive variation in yellowtail rockfish populations. Care must be taken, however, when interpreting and comparing results where macroscopic characteristics are used. While field assessments by microscopic staging of whole oocytes or macroscopic examinations are less time-consuming, validation by histological methods is required for precise and detailed information (West 1990). Furthermore, studies on the impact of atresia and postovulatory follicles are relevant to understanding functional relationships between yellowtail rockfish reproduction and their environment. West (1990) suggests histology as the appropriate method of use for these types of studies.

A prolonged reproductive season is characteristic of the genus *Sebastes*, but the factors regulating such a

mechanism are not clear. While temperature and photoperiod appear to effect later spawning in higher-latitude populations (Wootton 1984), inherent factors may also play a key role in the prolonged seasonality displayed by rockfishes. There is some evidence that age, at least in yellowtail rockfish, may account for some variation in parturition time within a season (M.J. Bowers, unpubl. data; Eldridge et al. 1991). In addition, Boehlert and Yoklavich (1984) estimated 5 days between hatching and birth in *S. melanops*, while parturition has been reported to occur immediately after hatching in the ovary in the subgenus *Sebasticus* (Tsu-kahara 1962). In this study, it could not be determined if hatched larvae remained in the ovaries of yellowtail rockfish. Further investigations are necessary to determine the occurrence, significance, and regulatory mechanisms of larval retention.

Rockfish are an important economic resource to the Washington, Oregon, and California fisheries. Estimates of total commercial rockfish landings in 1985 were 37,806 mt (PFMC 1990). In the same year, recreational anglers landed approximately 4000 mt of rockfish in California alone. Yellowtail, blue, and black rockfishes represented 30% of the recreational landings (Lenarz 1986). Fluctuations in year-class strength cause the fishery to be somewhat unpredictable (Lenarz 1986), leaving it difficult for optimal management strategies to protect stock depletion and establish harvest guidelines. The earlier one can predict recruitment success, the more precise management decisions are likely to be. Leaman (1988) discussed the value of directing management models toward biological principles. Responses of yellowtail rockfish ovaries to environmental fluctuations are early indicators of reproductive performance. This study documents the process of oocyte development in yellowtail rockfish and provides a basis for interannual comparisons.

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Effects of acute temperature change, *in vivo* and *in vitro*, on the acid–base status of blood from yellowfin tuna (*Thunnus albacares*)

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In most fishes, blood acid–base regulation following a temperature change involves active adjustments of gill ion-exchange rates which take hours or days to complete. Previous studies have shown that isolated blood from skipjack tuna, *Katsuwonus pelamis*, and albacore, *Thunnus alalunga*, had rates of pH change with temperature (in the open system) equivalent to those necessary to retain net protein charge *in vivo* ($\approx -0.016 \Delta\text{pH} \cdot ^\circ\text{C}^{-1}$). It was postulated that this is due to protons leaving the hemoglobin combining with plasma bicarbonate (HCO_3^-), which is removed as gaseous CO_2 , and that this ability evolved so that tunas need not adjust gill ion-exchange rates to regulate blood pH appropriately following ambient temperature changes. We reexamined this phenomenon using blood and separated plasma from yellowfin tuna, *Thunnus albacares*. Unlike previous studies, our CO_2 levels (0.5 and 1.5% CO_2) span those seen in yellowfin tuna arterial and venous blood. Various bicarbonate concentrations ($[\text{HCO}_3^-]$) were obtained by collecting blood from fully rested as well as vigorously exercised fish. We use our *in vitro* data to calculate basic physicochemical parameters for yellowfin tuna blood: nonbicarbonate buffering (β), the apparent first dissociation constant of carbonic acid (pK_{app}), and CO_2 solubility (αCO_2). We also determined the effects of acute temperature change on arterial pH, $[\text{HCO}_3^-]$, and partial pressures of O_2 and CO_2 *in vivo*. The pH shift of yellowfin tuna blood subjected to a closed-system temperature change did not differ from previous studies of other teleosts ($\approx -0.016 \Delta\text{pH} \cdot ^\circ\text{C}^{-1}$). The pH shift in blood subjected to open-system temperature change was PCO_2 dependent and lower than that in skipjack tuna or albacore blood *in vitro*, but identical with that seen in yellowfin tuna blood *in vivo*. However, pH adjustments *in vivo* were caused by changes in both $[\text{HCO}_3^-]$ and PCO_2 . The exact mechanisms responsible for these changes remain to be elucidated.

BRILL, R. W., BUSHNELL, P. G., JONES, D. R., et SHIMIZU, M. 1992. Effects of acute temperature change, *in vivo* and *in vitro*, on the acid–base status of blood from yellowfin tuna (*Thunnus albacares*). Can. J. Zool. 70: 654–662.

Chez la plupart des poissons, le contrôle acide–base du sang après un changement de température nécessite des ajustements importants des taux d'échange d'ions dans les branchies durant plusieurs heures ou jours. Des études antérieures ont démontré que dans du sang isolé de la Thonine à ventre rayé, *Katsuwonus pelamis*, et du Germon atlantique, *Thunnus alalunga*, les taux de changement du pH en fonction de la température (dans un système ouvert) étaient équivalents aux taux nécessaires au maintien de la charge nette des protéines *in vivo* ($\approx -0.016 \text{ pH} \cdot ^\circ\text{C}^{-1}$). Le phénomène a été expliqué de la façon suivante : les protons libérés par l'hémoglobine se combinent aux bicarbonates du plasma (HCO_3^-), qui sont libérés sous forme de CO_2 gazeux, et cette propriété permet aux thons de ne pas avoir à réajuster les taux d'échange d'ions dans leurs branchies pour maintenir le pH de leur sang après des changements de température ambiante. Nous avons réexaminé ce phénomène chez l'Albacore à nageoires jaunes, *Thunnus albacares*, en utilisant du sang et du plasma séparé. Contrairement aux résultats obtenus chez les autres poissons, les concentrations de CO_2 que nous avons observées (0,5% et 1,5% CO_2) se trouvent à l'intérieur des limites rencontrées normalement dans le sang artériel ou veineux de l'Albacore à nageoires jaunes. Des concentrations variées de bicarbonates ($[\text{HCO}_3^-]$) ont été obtenues dans des échantillons de sang prélevés chez des poissons parfaitement reposés et des poissons soumis préalablement à des exercices intenses. Nous utilisons ici nos données obtenues *in vitro* pour calculer les paramètres physico-chimiques de base dans le sang de l'Albacore à nageoires jaunes : capacité tampon due à des sels autres que les bicarbonates (β), constante de la première dissociation de l'acide carbonique apparente (pK_{app}) et solubilité du CO_2 (αCO_2). Nous avons également déterminé les effets d'un changement important de température sur le pH artériel, $[\text{HCO}_3^-]$, et les pressions partielles de O_2 et de CO_2 *in vivo*. Le changement de pH dans le sang d'Albacore à nageoires jaunes soumis à un changement de température en système fermé ne diffère pas de celui obtenu au cours d'études antérieures chez d'autres téléostéens ($\approx -0.016 \text{ pH} \cdot ^\circ\text{C}^{-1}$). Le changement de pH dans du sang exposé à des changements de température en système ouvert est fonction de la pression pCO_2 et moins important que les changements obtenus *in vitro* dans du sang de Thonines à ventre rayé ou de Germons atlantiques, mais identique au changement observé dans le sang d'Albacore à nageoires jaunes *in vivo*. Cependant, les ajustements de pH *in vivo* sont réalisés grâce à des changements de la concentration de $[\text{HCO}_3^-]$ et de la pression pCO_2 . Le mécanisme responsable de ces changements reste encore à déterminer.

[Traduit par la rédaction]

Introduction

Tunas (family Scombridae, tribe Thunnini) are unique among teleosts: they possess vascular countercurrent heat exchangers, can have deep red muscle temperatures as much as 20°C above ambient temperature (Carey *et al.* 1971), and have sustained muscle temperatures at least 2–3°C above ambient (Dizon and Brill 1979a, 1979b). The blood of tunas is therefore regularly subjected to closed-system (i.e., constant CO₂ content, variable CO₂ partial pressure (Pco₂)) temperature changes as it passes through the vascular countercurrent heat exchangers. In homeotherms, when the extremities are exposed to cold, blood returning to the core may be subjected to temperature changes of up to 30°C (Bazett *et al.* 1948; Gordon *et al.* 1982; Irving 1972). Because this is similar to the maximum temperature shifts to which the blood of tunas is exposed, there are no *a priori* reasons to suspect that tuna blood should show acid–base changes that are different from those exhibited by mammalian blood during *in vitro* closed-system temperature changes.

Unlike other fishes, which remain at preferred temperatures (Crawshaw 1975; Beiting and Fitzpatrick 1979; Reynolds and Casterlin 1979), tunas regularly subject themselves to rapid ambient temperature changes of 10°C or more during the vertical migrations that are a regular part of their daytime activity (Dizon *et al.* 1978; Holland *et al.* 1990). Such behavior exposes the blood within the gills to rapid open-system (i.e., constant Pco₂, variable CO₂ content) temperature changes. This unusual situation provides *a priori* reasons to suspect that tuna blood should show acid–base changes that differ from those exhibited by the blood of other teleosts during *in vitro* open-system temperature changes. As discussed by Somero (1986) and Cameron (1989a), intracellular pH and net protein charge are important factors in enzyme function. Therefore, exceptional mechanisms for regulation of net protein charge could be present in tuna blood.

The effects of temperature changes on *in vivo* and *in vitro* blood acid–base balance have been recently reviewed by Heisler (1984a, 1986), Truchot (1987), and Cameron (1989b). In general, ectothermic air-breathing animals regulate blood acid–base status, to maintain constant net protein charge, by adjusting Pco₂ in the arterial blood via changes in ventilation. In contrast, water breathers maintain blood acid–base status in the face of temperature changes via changes in blood bicarbonate concentration ([HCO₃⁻]). This involves regulation of gill ion-exchange rates (i.e., changes in the plasma strong ion difference (Stewart 1981)). Whereas changes in arterial Pco₂ in air-breathing animals can be accomplished within minutes, active adjustments of blood [HCO₃⁻] in water-breathing animals, via adjustment of gill ion-exchange rates, may take from several hours to 24 h (Heisler 1984b). These latter sorts of adjustments seem ill suited to tunas because of their regular and repeated exposure to rapid ambient temperature changes.

Perry *et al.* (1985a, 1985b) were the first to specifically investigate blood acid–base regulation in tunas, including the effects of *in vitro* temperature change. During closed-system temperature changes (15 – 30°C), they found that the true plasma pH¹ of skipjack tuna, *Katsuwonus pelamis*, exhibited

the expected rate of change ($-0.0165 \Delta \text{pH} \cdot ^\circ\text{C}^{-1}$) due to decreased solubility of CO₂ and reciprocal titration of plasma proteins and plasma HCO₃⁻. Surprisingly, Perry *et al.* (1985b) also found that the true plasma pH of skipjack tuna had a remarkably high rate of change ($-0.0131 \Delta \text{pH} \cdot ^\circ\text{C}^{-1}$) when subjected to open-system temperature changes (15 – 30°C). This large pH shift was due to a large change in plasma [HCO₃⁻] ($-0.34 \Delta \text{mM} \cdot ^\circ\text{C}^{-1}$) which, in turn, was presumed to be due to the release of protons from hemoglobin as the temperature increased. (In the open system, the released protons combine with plasma bicarbonate and it is removed as gaseous CO₂.) In similar *in vitro* experiments using blood from sand trout, *Cynoscion arenarius*, Cameron (1978) found much lower changes in true plasma pH ($-0.0048 \Delta \text{pH} \cdot ^\circ\text{C}^{-1}$) and [HCO₃⁻] ($-0.05 \Delta \text{mM} \cdot ^\circ\text{C}^{-1}$) during open-system temperature changes. Perry *et al.* (1985b) concluded that the high rate of $\Delta \text{pH} \cdot ^\circ\text{C}^{-1}$ seen in tuna blood *in vitro* was needed to maintain net protein charge *in vivo* during rapid ambient temperature changes. Cech *et al.* (1984), investigating the effects of temperature on the oxygen-binding characteristics of isolated blood of albacore, *Thunnus alalunga*, found identical rates of true plasma pH change ($-0.016 \Delta \text{pH} \cdot ^\circ\text{C}^{-1}$) during both open- and closed-system temperature changes (10 – 35°C). Therefore this tuna species also appears to be able to maintain net protein charge, in the face of rapid ambient temperature changes, without requiring adjustment of active gill ion pumps.

Perry *et al.* (1985b) used blood from captive fish immediately after they had been paralyzed with a neuromuscular blocking agent (gallamine triethiodide); no time was given for the fish to recover from the trauma of handling. Cech *et al.* (1984) used similar techniques, except that blood was taken from fish shortly after they had been boated, because, at that time, albacore had never been successfully returned to shore-side tanks. Techniques for the anaesthetization, catheterization, recovery, and maintenance of catheterized tunas have subsequently been developed (Jones *et al.* 1986; Bushnell 1988). Blood samples can now be taken for *in vivo* studies or large quantities collected for *in vitro* studies from tunas that are fully recovered (i.e., have normal blood acid–base status) and that can make appropriate cardiorespiratory adjustments to environmental changes (e.g., changes in ambient oxygen levels; Bushnell *et al.* 1990; Bushnell and Brill 1991).

The present study investigated the changes in arterial pH, [HCO₃⁻], Pco₂, and O₂ partial pressure (Po₂) in yellowfin tuna, *Thunnus albacares*, exposed to acute temperature changes. The time course of the temperature changes, and the temperatures used (25 – 20°C and 25 – 18°C), match those to which small yellowfin tuna near Hawaii normally subject themselves (Holland *et al.* 1990). Also, in an attempt to understand the mechanisms driving the changes observed *in vivo*, we determined the rates of pH, [HCO₃⁻], and Pco₂ change using whole blood and separated plasma subjected to open- and closed-system temperature changes *in vitro*.

For the *in vitro* studies, we used blood taken from fish that had been vigorously exercised, as well as from those that had fully recovered from handling and surgery. Using blood from exercised and fully recovered animals affords comparison with previous studies and provides a range of initial plasma [HCO₃⁻]. Furthermore, unlike previous studies, we employed Pco₂ levels that bracket the arterial and venous Pco₂ levels observed in swimming tunas (Jones *et al.* 1986). We also

¹The pH measured when whole blood is equilibrated to a given gas mixture, or withdrawn directly from an animal, and then injected into the pH electrode.

gathered data that allow the calculation of basic physiochemical parameters (nonbicarbonate buffering (β), the apparent first dissociation constant of carbonic acid (pK_{app}), and CO_2 solubility (αCO_2)) and the construction of $pH-HCO_3^-$ (i.e., Davenport) diagrams specific to yellowfin tuna blood. These are needed for interpreting data from this and future studies on the effects of temperature and exercise on the blood acid-base status of tunas *in vivo* and *in vitro*.

Materials and methods

Yellowfin tunas were purchased from local commercial fishermen and maintained in outdoor tanks (at $25 \pm 2^\circ C$) at the Kewalo Research Facility (Southwest Fisheries Science Center Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration). Fish were held in captivity for a few days to several months before use. Food was presented daily, but fish were not fed for at least 20 h prior to use in an experiment to allow sufficient time for gut clearance (Magnuson 1969). A total of 24 animals, ranging in weight from 1.4 to 2.6 kg, were used.

In vitro studies

To obtain blood for *in vitro* studies from animals whose condition approximated that of fish used by Perry *et al.* (1985a) and Cech *et al.* (1984) (henceforth referred to as "exercised"), fish were vigorously chased in their holding tank, netted, and stunned by a blow to the head. Approximately 20–40 mL of blood was then withdrawn by direct cardiac puncture and immediately mixed with 2000 IU of sodium heparin (0.2 mL of 10 000 IU $\cdot$ mL $^{-1}$).

To obtain blood from rested animals (henceforth referred to as "normal"), fish were dip netted and immediately anaesthetized by being placed in a plastic bag containing tricaine methanesulfonate ($1 \text{ g} \cdot \text{L}^{-1}$) buffered with an equal molar concentration of $NaHCO_3$. After initial anaesthetization, individual fish were moved to the laboratory and suspended on a surgical table in a chamois sling. A hose with running seawater was placed in the mouth, and oxygenated seawater, containing $0.1 \text{ g} \cdot \text{L}^{-1}$ of $NaHCO_3$ buffered tricaine methanesulfonate and chilled to approximately $22^\circ C$, was pumped over the gills. Both anaesthetic solutions were bubbled vigorously for at least 1 h prior to use to remove excess CO_2 . While the fish was still anaesthetized, an 18 or 20 gauge Teflon catheter was introduced into either the ventral or dorsal aorta under manometric guide as described in Jones *et al.* (1986). A length of PE 160 tubing was connected to the catheter and was led out of the mouth through a hole made in the snout (for dorsal aorta catheterization) or simply sutured to the skin (for ventral aorta catheterization). At the completion of surgery, a 22 gauge hypodermic needle was inserted through the dorsal body musculature and into the neural canal immediately behind the skull. The needle was used for injection of 2% lidocaine hydrochloride. This procedure paralyzes all of the spinal motor nerves but apparently leaves all cranial nerves intact (Bushnell *et al.* 1990). The fish was then fixed under water in front of a pipe delivering air-saturated ($25^\circ C$) fresh seawater at approximately $35 \text{ L} \cdot \text{min}^{-1}$. Tunas maintained like this recover from anaesthesia within minutes, are able to control their own ventilation volumes, and will survive in good condition for up to 12 h (Bushnell *et al.* 1990).

Beginning approximately 1 h after surgery, ≈ 0.3 -mL blood samples were periodically taken to check the true plasma pH. It generally took 1–3 h following surgery for the true plasma pH to return to a value considered normal in swimming tunas (≈ 7.7 – 7.8 ; Jones *et al.* 1986). Once it had reached this level, approximately 20–40 mL of blood was withdrawn as quickly as possible and with minimal disturbance to the fish. Samples were immediately pooled and mixed with 2000 IU of sodium heparin (0.2 mL of 10 000 IU $\cdot$ mL $^{-1}$). The fish was then promptly sacrificed with a massive overdose of sodium pentobarbital.

Immediately after the blood was obtained, a 1-mL sample was centrifuged, and 0.2 mL of the resultant plasma mixed with cold 8%

perchloric acid to precipitate plasma proteins. This mixture was centrifuged and the resultant supernatant stored frozen ($-4^\circ C$) for a maximum of about 6 months before lactate analysis. Lactate concentrations were determined using standard techniques (Sigma Chemical Co., St. Louis, Mo., kit 825-UV). Samples of whole blood were also taken at this time for measurement of hematocrit.

Two-millilitre samples of blood were placed in four glass tonometers. Two of the tonometers were kept in a temperature-controlled water bath maintained at $20^\circ C (\pm 0.2^\circ C)$ and two in a temperature-controlled water bath maintained at $30^\circ C (\pm 0.2^\circ C)$. One tonometer in each bath was supplied with air (saturated with water vapor) containing 0.5% CO_2 ; the other tonometer in each water bath was supplied with air (saturated with water vapor) containing 1.5% CO_2 . Precise CO_2 levels in the gas mixtures were obtained using two Wösthoff gas mixing pumps, connected in series, to add pure (99.5%) CO_2 to air. The resultant gas mixtures were stored in automobile tire inner tubes.

The remaining blood was centrifuged and the resultant plasma (i.e., separated plasma) either stored at $\approx 3^\circ C$ in a refrigerator or placed in a second set of tonometers in the water baths. These tonometers were also supplied with water vapor saturated air containing 0.5 or 1.5% CO_2 . In experiments in which the separated plasma was stored overnight, it was allowed to warm slowly to room temperature the next morning and was then placed in the tonometers.

All tonometers were equilibrated for at least 1 h with their gas mixtures, at the appropriate temperatures, before the blood or separated plasma samples were introduced. Approximately 1 h after the blood or separated plasma samples were placed in the tonometers, ≈ 0.2 -mL subsamples were withdrawn, in random order, and the pH was measured using two Radiometer MKS Mark 2 blood gas analyzers whose pH (and P_{CO_2}) electrodes were maintained at either 20 or $30^\circ C$. The effects of closed-system temperature changes on pH were measured by injecting the blood or separated plasma equilibrated at $20^\circ C$ into the pH electrode maintained at $30^\circ C$, and vice versa. The pH of the true plasma and separated plasma were measured 2–5 times, depending on the consistency of the readings, and the results averaged. The effect of closed-system temperature change on P_{CO_2} was measured by analyzing the blood and separated plasma equilibrated at $20^\circ C$ in the P_{CO_2} electrode maintained at $30^\circ C$. The pH electrodes were calibrated with pH 7.00 and 8.00 buffers and the P_{CO_2} electrode at two points using precision gas mixtures.

At the end of the experiment, ≈ 0.4 -mL samples were taken for measurement of the total CO_2 concentration. Blood samples were placed in 3-mL Eppendorf tubes, under mineral oil, and centrifuged at room temperature. The resultant anaerobically isolated plasma (i.e., true plasma) was analyzed using the technique described in Cameron (1971). The total CO_2 concentration of separated plasma was measured using the same technique, but samples to be analyzed were taken directly from the tonometers.

The solubility of CO_2 (αCO_2 , mM $\cdot$ mmHg $^{-1}$) in acidified yellowfin tuna plasma ($pH = 3.1$) was measured at 15, 20, 25, and $30^\circ C$ after being equilibrated with water vapor saturated 99.5% CO_2 as described by Boutilier *et al.* (1985). Mean measured αCO_2 for yellowfin tuna plasma was used in all calculations. True and separated plasma $[HCO_3^-]$ (mM) were calculated by subtracting the quantity of dissolved CO_2 ($\alpha CO_2 \times P_{CO_2}$) from measured total CO_2 . The pK_{app} for true and separated plasma was calculated using measured variables and the Henderson-Hasselbalch equation:

$$[1] \quad pK_{app} = pH - \frac{\log[HCO_3^-]}{\alpha CO_2}$$

To avoid false replicates and to minimize variability, all variables were calculated individually for each fish and then averaged. All mean values are given $\pm$ standard error of the mean (SEM). All pairwise comparisons used the two-tailed Student's *t*-test; all multiple comparisons used the nested factorial analysis of variance design. $P < 0.05$ was taken as the minimum level for significant differences.

TABLE 1. Effects of PCO_2 , vigorous exercise, and temperature on acid-base status and pK_{app} of isolated yellowfin tuna blood and plasma

	0.5% CO_2		1.5% CO_2	
	20°C	30°C	20°C	30°C
Normal fish				
pH_{tp}	7.923 ± 0.032 (8)	7.842 ± 0.024 (7)	7.643 ± 0.029 (8)	7.585 ± 0.022 (8)
pH_{sp}	7.999 ± 0.025 (8)	8.002 ± 0.021 (8)	7.602 ± 0.020 (8)	7.634 ± 0.019 (8)
$[HCO_3^-]_{tp}$	13.0 ± 1.2 (8)	10.4 ± 0.7 (7)	18.0 ± 1.37 (8)	14.2 ± 1.0 (8)
$[HCO_3^-]_{sp}$	13.0 ± 0.7 (8)	12.4 ± 0.9 (8)	15.0 ± 0.8 (8)	14.0 ± 0.8 (8)
$pK_{app, tp}$	6.06 ± 0.02 (8)	5.96 ± 0.02 (7)	6.11 ± 0.01 (8)	6.05 ± 0.02 (8)
$pK_{app, sp}$	6.11 ± 0.01 (8)	6.05 ± 0.02 (8)	6.14 ± 0.01 (8)	6.10 ± 0.01 (8)
Exercised fish				
pH_{tp}	7.493 ± 0.030 (4)	7.395 ± 0.030 (4)	7.333 ± 0.020 (4)	7.286 ± 0.026 (4)
pH_{sp}	7.770 ± 0.038 (5)	7.752 ± 0.036 (5)	7.451 ± 0.049 (5)	7.452 ± 0.040 (5)
$[HCO_3^-]_{tp}$	4.1 ± 0.3 (4)	3.1 ± 0.2 (4)	7.1 ± 0.2 (4)	6.1 ± 0.5 (4)
$[HCO_3^-]_{sp}$	6.8 ± 0.51 (5)	6.5 ± 0.6 (5)	9.3 ± 0.7 (5)	7.5 ± 0.4 (5)
$pK_{app, tp}$	6.11 ± 0.03 (4)	6.03 ± 0.02 (4)	6.19 ± 0.01 (4)	6.15 ± 0.02 (4)
$pK_{app, sp}$	6.18 ± 0.02 (5)	6.08 ± 0.02 (5)	6.19 ± 0.02 (5)	6.19 ± 0.03 (5)

NOTE: Numbers of observations are shown in parentheses; tp, true plasma; sp, separated plasma.

TABLE 2. Effects of acute temperature change on acid-base status and pK_{app} of yellowfin tuna blood *in vivo*

	25°C	20°C	18°C
pH_{tp}	7.800 ± 0.010 (11)	7.890 ± 0.015 (5)	7.850 ± 0.013 (6)
PO_2			
mmHg	52.1 ± 2.7 (6)	—	79.2 ± 4.8 (6)
kPa	6.95 ± 0.36 (6)	—	10.6 ± 0.64 (6)
PCO_2			
mmHg	5.4 ± 0.2 (11)	4.5 ± 0.2 (5)	3.9 ± 0.07 (6)
kPa	0.73 ± 0.03 (11)	0.60 ± 0.03 (5)	0.52 ± 0.01 (6)
$[HCO_3^-]_{tp}$ (mM)	12.2 ± 0.6 (6)	—	13.5 ± 0.5 (6)
$pK_{app, tp}$	6.02 ± 0.02 (6)	—	5.97 ± 0.01 (6)

NOTE: Numbers of observations are shown in parentheses; tp, true plasma.

In vivo studies

Fish for *in vivo* studies were treated essentially as described above for obtaining blood from fully recovered animals. The only differences were that only the dorsal aorta was catheterized and that the fish were not injected with heparin. After the interval of several hours required for a fish to recover from surgery and for the true plasma pH to return to normal, samples were taken for measurement of lactate and hematocrit (as described above). Following this, 6 fish (mean weight 1.29 ± 0.16 kg) were subjected to a series of step changes in water temperature between 25 and 20°C and 6 fish (mean weight 1.24 ± 0.14 kg) from 25 to 18°C by cooling or warming the water presented to the fish's mouth. Individual fish were subjected to 4 or 5 temperature changes and were maintained at 18 or 20°C for a maximum of 25 min. Between cooling cycles fish were held at 25°C for 30 min.

Arterial blood samples were taken for analysis of true plasma pH, PCO_2 , HCO_3^- (as described above), and PO_2 a few minutes prior to, and 15 and 20 min after, the completion of each temperature change. The cooling cycle was effected in 3 min and the warming cycle took 5–10 min. Blood PO_2 was measured using two Radiometer MKS Mark 2 blood gas analyzers, one with the PO_2 electrode maintained at 18 or 20°C and the other with the electrode at 25°C. The PO_2 electrodes were calibrated at 18, 20, and 25°C with a standard zero PO_2 solution and air-equilibrated saline.

To minimize any effects of changes in blood acid-base parameters

occurring over time, and the variability between animals, results were calculated separately for each temperature and each temperature change and then averaged.

Results

The pH, $[HCO_3^-]$, and pK_{app} values of true and separated plasma from *in vitro* samples are given in Table 1; those from *in vivo* samples (plus mean PO_2 values) are given in Table 2. Mean plasma lactate levels for normal and exercised fish (4.6 ± 1.6 and 8.8 ± 2.6 mM, respectively) were not significantly different. Blood samples taken from fish used in the *in vivo* studies had a mean plasma lactate level (3.0 ± 0.3 mM) not significantly different from blood of normal fish. However, when comparisons were made at the same PCO_2 values and equilibration temperatures, $[HCO_3^-]$ in true and separated plasma from exercised fish was significantly lower than in the other two groups. Mean hematocrits in blood from exercised and normal fish and fish used in the *in vivo* studies (40.6 ± 4.7 , 33.4 ± 1.2 , and $34.2 \pm 1.2\%$, respectively) were not significantly different.

The effect of temperature on αCO_2 in acidified yellowfin tuna plasma is shown in Fig. 1. The αCO_2 curve for rainbow

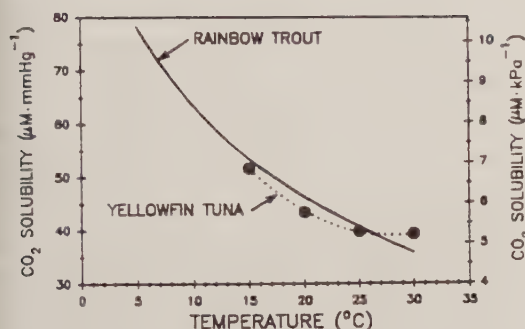


FIG. 1. Effects of temperature on CO_2 solubility in acidified yellowfin tuna plasma and acidified rainbow trout plasma. Data for rainbow trout are from Boutilier *et al.* (1985).

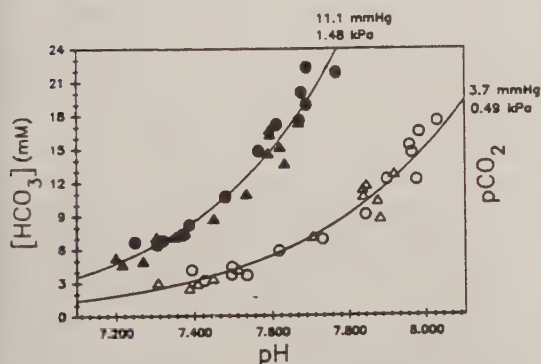


FIG. 2. A $\text{pH}-\text{HCO}_3^-$ (i.e., Davenport) diagram for yellowfin tuna blood equilibrated to 0.5% CO_2 ($P_{\text{CO}_2} = 3.7$ mmHg or 0.49 kPa) at 20°C (○) and 30°C (Δ), and to 1.5% CO_2 ($P_{\text{CO}_2} = 11.1$ mmHg or 1.48 kPa) at 20°C (●) and 30°C (▲). $[\text{HCO}_3^-]$ was measured in true plasma anaerobically separated at room temperature. Lines, added simply for illustrative purposes, were fitted using a nonlinear least-squares regression.

trout (*Oncorhynchus mykiss*) plasma (from Boutilier *et al.* 1985, extrapolated from 15 to 30°C) is plotted for comparison. The equation for a second-degree polynomial fit to the tuna data is

$$[2] \alpha\text{CO}_2 = 98.855 \pm 2.827 - 4.2830 \pm 0.2629 \times T + T + 0.0770 \pm 0.0058 \times T^2, r^2 = 0.9996$$

(Regression parameters are given $\pm$ their standard deviation.)

Nonbicarbonate buffering values (β , $\Delta[\text{HCO}_3^-] \cdot \Delta\text{pH}^{-1}$, or Slykes) were calculated for true and separated plasma for each fish and then averaged. Mean β values for true or separated plasma from exercised and normal fish did not differ significantly, so data were combined. Mean β values were -20.9 ± 1.2 and $-5.1 \pm 0.7 \Delta\text{mM} \cdot \Delta\text{pH}^{-1}$ for true and separated plasma, respectively.

All data on true plasma pH and $[\text{HCO}_3^-]$ from exercised and normal fish are plotted as a $\text{pH}-\text{HCO}_3^-$ diagram (Fig. 2). Data for blood equilibrated at 20 and 30°C have been combined and iso- P_{CO_2} lines (0.5% $\text{CO}_2 = 3.7$ mmHg or 0.49 kPa P_{CO_2} and 1.5 $\text{CO}_2 = 11.1$ mmHg or 1.48 kPa P_{CO_2}) fitted to

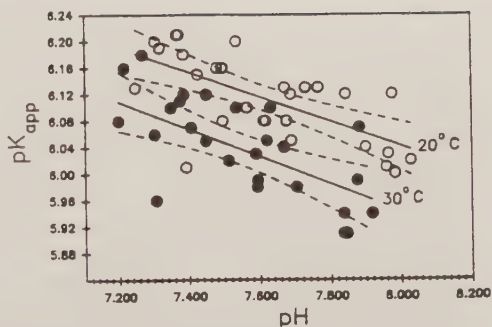


FIG. 3. Effects of temperature and pH on the pK_{app} of yellowfin tuna true plasma. The pK_{app} was calculated from measured variables and the Henderson-Hasselbalch equation. Open circles represent blood equilibrated to 20°C and solid circles blood equilibrated to 30°C. Regression lines were fitted separately for data collected at each temperature. Broken lines show the 95% confidence intervals of the regression lines.

the data, using least-squares nonlinear regression, simply for illustrative purposes.

The effects of pH and temperature on pK_{app} or yellowfin tuna true plasma are shown in Fig. 3. Linear regression equations 3 and 4 were fitted separately to the data collected at 20 and 30°C, respectively; regression lines ($\pm 95\%$ confidence intervals) are also presented in Fig. 3.

$$[3] \text{pK}_{\text{app}} = -0.187 \pm 0.040 \times \text{pH} + 7.534 \pm 0.307, r = 0.629$$

$$[4] \text{pK}_{\text{app}} = -0.207 \pm 0.053 \times \text{pH} + 7.599 \pm 0.400, r = 0.615$$

(Regression parameters are given $\pm$ their standard deviation.)

In addition, a regression equation relating true plasma pH, pK_{app} , and temperature (°C) was calculated using an iterative procedure (Systat nonlinear estimation procedure). The data were fitted to a model similar to that used by Boutilier *et al.* (1985):

$$[5] \text{pK}_{\text{app}} = 7.228 \times T^{-0.01546} + \log T \times (0.4513 - 0.04699 \times \text{pH}) - 0.04578 \times \text{pH} + 0.1582$$

Effects of temperature change in vitro

The effects of exercise and P_{CO_2} on $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ of true and separated plasma during open- and closed-system temperature changes are shown in Fig. 4. Temperature affects the pH of true plasma and separated plasma very differently during open-system (i.e., constant P_{CO_2} , variable CO_2 content) temperature changes. A nested factorial analysis of variance showed no significant differences in $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ of samples taken from normal and exercised fish. There were, as expected, clearly significant differences in $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ of true and separated plasma, and a significant effect of CO_2 on $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$.

The $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ exhibited by both true and separated plasma was significantly greater during closed-system temperature changes (Fig. 4). The factorial analysis of variance performed on these data showed no significant differences in $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ between samples from exercised and normal fish or between true and separated plasma, or between CO_2 levels.

1 and 2) is approximately 2–4 times that reported for other teleosts *in vivo* ($\approx 4\text{--}7\text{ mM}$; Cameron 1978) and is significantly higher than that measured in isolated (tonometered with 1% CO_2) skipjack tuna blood ($\approx 8\text{ mM}$ at 20°C and $\approx 5\text{ mM}$ at 30°C ; Perry *et al.* 1985a). This implies that the blood samples collected by Perry *et al.* (1985a) were from fish that had not fully recovered from the effects of transfer from their holding tank to the laboratory and the procedures required to implant the ventral aorta catheters.

The nonbicarbonate buffering capacity of yellowfin tuna blood ($-20.9\Delta[\text{HCO}_3^-] \cdot \Delta\text{pH}^{-1}$) is the highest yet recorded in any teleost, being approximately twice that measured in other fishes (e.g., rainbow trout; Wood and Jackson 1980), including skipjack tuna (Perry *et al.* 1985a). This could be explained by the high hemoglobin content of yellowfin tuna blood (Brill and Bushnell 1991), although skipjack tuna blood has equally elevated hemoglobin levels (Brill and Bushnell 1991) but lower nonbicarbonate buffering capacity. The large decrease in true plasma bicarbonate and pH seen in samples from exercised fish (Table 1) might therefore seem surprising at first, given the high nonbicarbonate buffering capacity of yellowfin tuna blood. However, tunas have a well-known capacity for extreme levels of white muscle anaerobic glycolysis and can achieve some of the highest white muscle lactate levels of any vertebrate species (Guppy *et al.* 1979).

The solubility of CO_2 in acidified tuna plasma appears to be slightly less than in acidified trout plasma. This may be due to the higher ion levels of the former (Saither and Rogers 1967; Boutilier *et al.* 1985; Bourke 1987). However, the CO_2 solubility data presented for trout plasma are extrapolated far outside the measurement temperature range, and direct comparison is probably not justified.

The effects of temperature and pH on pK_{app} can be clearly seen in Fig. 3. The effect of pH on pK_{app} is greater in yellowfin tuna true plasma than in the rainbow trout true plasma studied by Boutilier *et al.* (1985). The slope of the $\text{pH}/\text{pK}_{\text{app}}$ regression line (at 15°C , the highest temperature used) is -0.080 in trout true plasma, but -0.17 (at 20°C , eq. 3) in yellowfin true plasma. However, the effect of temperature on pK_{app} ($\Delta\text{pK}_{\text{app}} \cdot ^\circ\text{C}^{-1}$) in tuna true plasma was less than that in rainbow trout true plasma. Using regression eqs. 3 and 4, $\Delta\text{pK}_{\text{app}} \cdot ^\circ\text{C}^{-1}$ was found to be -0.008 and -0.009 at pH 7.4 and 8.0, respectively. Similarly determined values for rainbow trout true plasma (Boutilier *et al.* 1985) were -0.016 and -0.021 at pH 7.4 and 8.0, respectively. The reasons for the differences in the effect of temperature on pK_{app} are unknown, but the differences are not due to methodology, since the techniques used by Boutilier *et al.* (1985) and in this study were essentially identical.

Table 1 also shows differences when pK_{app} is determined by tonometering whole blood and measuring the pH of true plasma versus tonometering and measuring pH of the separated plasma. These differences are most likely due to the effects of anaerobic centrifugation of blood at room temperature rather than at the equilibration temperature, and the "hemolysis effect" of red cells on true plasma pH measurements. The importance of these effects and the inherent errors in measuring Pco_2 , $[\text{HCO}_3^-]$, and pH have been reviewed recently by Boutilier *et al.* (1985) and will not be repeated here.

The effects of temperature on the pH of true plasma and separated plasma

That red blood cells are involved in the pH changes seen during open-system temperature change is obvious from

Fig. 4. Clearly, the red cells are exchanging something with the plasma that causes a change in true plasma $[\text{HCO}_3^-]$ and in turn, a change in pH. Perry *et al.* (1985a) assumed that the reduction in true plasma $[\text{HCO}_3^-]$ seen during open-system temperature change in skipjack tuna blood was due to protons leaving the hemoglobin, combining with plasma bicarbonate and removing it as gaseous CO_2 . However, this effect could also have been due to net bicarbonate uptake by the cell or to exchange of strong ions between the plasma and red cells resulting in a change in plasma strong ion difference (Stewart 1981; Cameron and Iwama 1987; Cameron 1989a). What exactly is being exchanged between the red cells and plasma was not determined by Perry *et al.* (1985a) or by us.

The effect of open-system temperature change on the pH of yellowfin tuna true plasma was unusually great ($\approx -0.016\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$) compared with similar observations made on the isolated blood of other teleosts ($-0.0048\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$; Cameron 1978), but this occurred only when the blood was equilibrated to the lower CO_2 level. The smaller $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ seen in yellowfin tuna true plasma equilibrated to 1.5% CO_2 is due to the steeper slope of the $\text{pH}/[\text{HCO}_3^-]$ line (Fig. 2) at this higher CO_2 level. In other words, when the blood is equilibrated to higher Pco_2 , equivalent changes in $[\text{HCO}_3^-]$ (Fig. 5) at constant Pco_2 result in smaller changes in true plasma pH (Fig. 4) because of the steeper slope of the $\text{pH}/[\text{HCO}_3^-]$ line (Fig. 2).

The $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ of isolated yellowfin tuna true plasma equilibrated with 1.5% CO_2 is less than that observed in isolated skipjack tuna blood equilibrated to 1% CO_2 . This difference is apparently due to the fact that Perry *et al.* (1985a) used blood taken from fish immediately after surgery. In skipjack tuna true plasma, $[\text{HCO}_3^-]$ was lower (total CO_2 was only $\approx 8\text{ mM}$ at 20°C), therefore the blood was operating on the flat portion of the $\text{pH}/[\text{HCO}_3^-]$ curve (Fig. 2), where relatively small changes in $[\text{HCO}_3^-]$ cause relatively larger changes in pH.

Perry *et al.* (1985a) assumed that the large $\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$ seen in isolated skipjack tuna true plasma was necessary to adjust pH appropriately *in vivo* in the face of rapid ambient temperature changes. They assumed that skipjack tuna must retain a constant relative blood alkalinity ($-0.016\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$) during rapid temperature changes. Although some teleosts do appear to regulate pH to retain a constant relative alkalinity, others do not (Truchot 1987), and there are no *a priori* reasons to assume that skipjack tuna would do so. Unfortunately, no data are available on the effects of rapid ambient temperature changes on the blood pH of skipjack tuna *in vivo*, so Perry *et al.*'s (1985a) hypothesis that skipjack tuna adjust blood pH without adjusting gill ion-exchange rates remains untested.

Effects of temperature change *in vivo*

Our data show that arterial true plasma pH changes ($-0.0105 \pm 0.0010\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$) *in vivo* match those found *in vitro* ($-0.0103 \pm 0.0008\Delta\text{pH} \cdot ^\circ\text{C}^{-1}$) at 0.5% CO_2 (i.e., at the Pco_2 approximating arterial Pco_2). Therefore, at first glance, our data do appear to support the hypothesis of Perry *et al.* (1985a) that tunas need not actively adjust plasma $[\text{HCO}_3^-]$, via changes in gill ion-exchange rates, to regulate blood pH following ambient temperature changes. However, Fig. 5 shows that true plasma $\Delta[\text{HCO}_3^-] \cdot ^\circ\text{C}^{-1}$ values *in vivo* are significantly lower than those observed *in vitro* in blood from normal fish. In other words, red blood cells appear to respond somewhat differently to temperature changes under

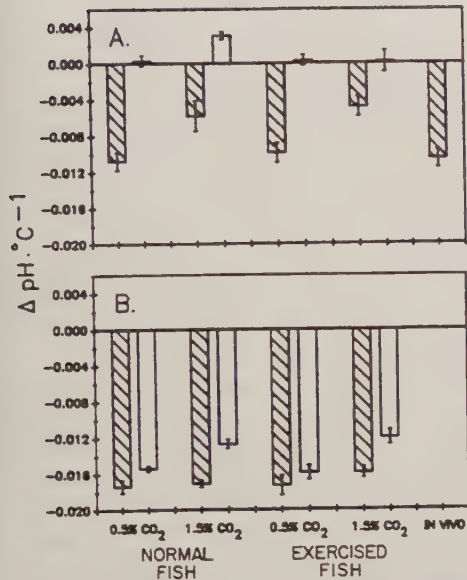


FIG. 4. Rates of pH change *in vitro* in true plasma (hatched bars) and separated plasma (open bars) for normal and exercised yellowfin tuna during (A) open-system (constant P_{CO_2} , variable CO_2 content) and (B) closed-system (constant CO_2 content, variable P_{CO_2}) temperature changes. True plasma pH changes (arterial blood samples) with temperature occurring *in vivo* are also shown in A.

The effects of open-system temperature changes on the $[\text{HCO}_3^-]$ of true plasma and separated plasma are shown in Fig. 5. The factorial analysis of variance performed on these data showed significant differences in $\Delta[\text{HCO}_3^-] \cdot ^\circ\text{C}^{-1}$ between samples from normal and exercised fish, and significant differences between true plasma and separated plasma. There was no significant effect of P_{CO_2} .

The effects of closed-system temperature changes on P_{CO_2} of blood and isolated plasma are shown in Fig. 6. The factorial analysis of variance performed on these data showed no significant differences in the behavior of samples taken from exercised and normal fish. There were, however, significant differences in $\Delta P_{\text{CO}_2} \cdot ^\circ\text{C}^{-1}$ between blood and separated plasma, and significant differences due to the P_{CO_2} to which the blood or separated plasma was originally equilibrated.

Effects of temperature change *in vitro*

The effects of rapid temperature changes on the arterial blood acid-base status are also shown in Table 2 and Figs. 4, 5, and 6. From the figures it is readily apparent that although the pH change *in vivo* matches that seen *in vitro* during open-system temperature changes at arterial (i.e., 0.5%) P_{CO_2} levels, the mechanisms driving these pH changes are different. Note that the change in $[\text{HCO}_3^-]$ observed *in vivo* is roughly half that observed *in vitro* in the true plasma obtained *in vivo* matches that observed *in vitro* (closed system) at equivalent starting P_{CO_2} and $[\text{HCO}_3^-]$ levels (i.e., normal blood equilibrated with 0.5% CO_2). Also, arterial P_{CO_2} changes in an opposite direction to arterial P_{O_2} : at lower temperatures the former decreases and the latter increases.

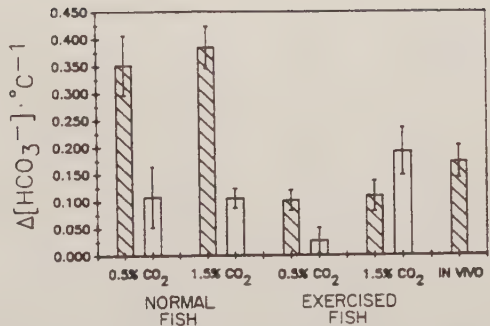


FIG. 5. Effects of *in vitro* open-system temperature changes on $[\text{HCO}_3^-]$ of true plasma (hatched bars) and separated plasma (open bars) from normal and exercised yellowfin tuna. The effects of *in vivo* temperature changes on true plasma $[\text{HCO}_3^-]$ (in arterial blood samples) are also shown.

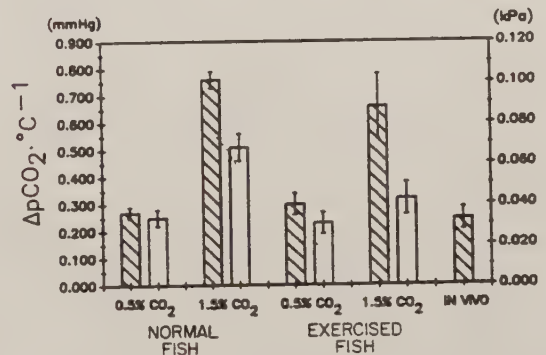


FIG. 6. Effects of closed-system temperature changes on P_{CO_2} of whole blood (hatched bars) and separated plasma (open bars) from normal and exercised yellowfin tuna. P_{CO_2} changes in arterial blood occurring *in vivo* are also shown.

Discussion

The pH values of both true and separated plasma at both equilibration temperatures and at both CO_2 levels are clearly lower in exercised fish than in normal fish. This is due to the plasma $[\text{HCO}_3^-]$ in the samples from exercised fish being approximately half that in samples from normal fish (Table 1 and Fig. 2). Note that the significant reductions in plasma $[\text{HCO}_3^-]$ occurred despite the absence of a significant elevation of plasma lactate. This suggests that protons may be released from the white muscle of yellowfin tuna unaccompanied by lactate, but proof of this phenomenon would require measurement of more parameters than was done for this study (Cameron and Cech 1990). White muscle lactate retention has been observed in other teleosts (Wardle 1978), including skipjack tuna (Perry *et al.* 1985a). The change in acid-base status of true plasma due to strenuous exercise ($\Delta \text{pH} \approx 0.4$ units) was similar to that observed in skipjack tuna (Perry *et al.* 1985a) and other teleosts following exhaustive activity (Wood *et al.* 1977; Turner *et al.* 1983).

The $[\text{HCO}_3^-]$ in true plasma from normal yellowfin tuna *in vitro* and in true plasma taken directly from live fish (Tables

these two conditions. Clearly, it is the increase in arterial PCO_2 observed *in vivo* that accounts for the observed equality of $\Delta pH \cdot ^\circ C^{-1}$ (Fig. 4) in spite of the differences in $\Delta [HCO_3^-] \cdot ^\circ C^{-1}$ (Fig. 5).

An increase in blood PCO_2 with increasing temperature is commonly observed in aquatic gill-breathing animals, although the magnitude of the increase is quite variable between species (Heisler 1986). As explained in detail by Randall and Cameron (1973), if fish were to increase arterial blood PCO_2 (and therefore decrease blood pH) by decreasing ventilation volume at higher temperatures, a concomitant decrease in arterial PO_2 would be expected. Because this is what we have observed in tunas *in vivo* (Table 2), it is possible that yellowfin tuna are indeed decreasing ventilation volume (or increasing gill resistance to O_2 and CO_2 transfer) as temperature increases, and are therefore compromising O_2 delivery to adjust blood pH. However, as explained in Truchot (1987), it is unlikely that gill-breathing animals can regulate PCO_2 via changes in ventilation.

In fishes, it appears that the dehydration of HCO_3^- (i.e., conversion of HCO_3^- to physically dissolved CO_2) is the rate-limiting step in CO_2 excretion (Perry 1986). As explained by Perry and Wood (1989), factors that reduce the rate of HCO_3^- dehydration (such as elevated circulating catecholamine levels post exercise) increase arterial blood PCO_2 . Because the rate of HCO_3^- dehydration is most likely directly proportional to temperature, increases in temperature would be expected to cause decreases in arterial PCO_2 , the exact opposite to what is observed *in vivo*.

In summary, the changes in arterial blood pH observed in yellowfin tuna *in vivo* resulting from rapid shifts in ambient temperature are due in part to changes in plasma $[HCO_3^-]$ caused by the red blood cells. They are also due in part to alterations of arterial blood PCO_2 . More research is clearly needed to determine the exact mechanisms responsible for both of these adjustments.

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NOTES

Gluconeogenesis in hepatocytes isolated from the skipjack tuna (*Katsuwonus pelamis*)

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BUCK, L. T., BRILL, R. W., and HOCHACHKA, P. W. 1992. Gluconeogenesis in hepatocytes isolated from the skipjack tuna (*Katsuwonus pelamis*). Can. J. Zool. 70: 1254–1257.

Skipjack tuna (*Katsuwonus pelamis*) hepatocytes were isolated and determined to be viable based on trypan blue exclusion, energy charge, and lactate dehydrogenase leakage. Trypan blue staining and red blood cell contamination were always less than 0.1%, and lactate dehydrogenase leakage remained less than 1% at 25°C for 10 h. The energy charge for freshly isolated cells ranged from 0.65 to 0.74. Alanine (10 mM) gave higher rates of gluconeogenesis and oxidation than lactate: alanine rates were 3.17 ± 0.65 $\mu\text{mol glucose}/(\text{g packed cells} \cdot \text{h})$ and 9.1 ± 1.19 $\mu\text{mol CO}_2/(\text{g} \cdot \text{h})$, whereas lactate rates were 0.47 ± 0.08 and 1.8 ± 0.27 , respectively. Phosphoenolpyruvate carboxykinase was 30% cytosolic and 70% mitochondrial, a finding that is in agreement with the liver's ability to use both lactate and alanine as gluconeogenic substrates. If hepatic gluconeogenesis is the major route of lactate removal postexercise, it is estimated that recovery would require 3800 h! Therefore, tuna liver is not the major site of glucose resynthesis and lactate clearance following burst exercise.

BUCK, L. T., BRILL, R. W., et HOCHACHKA, P. W. 1992. Gluconeogenesis in hepatocytes isolated from the skipjack tuna (*Katsuwonus pelamis*). Can. J. Zool. 70: 1254–1257.

Des hépatocytes de Thons à ventre rayé (*Katsuwonus pelamis*) ont été isolés et identifiés comme viables ou non viables par examen de l'excrétion de bleu trypan, de la charge énergétique et de la fuite de lactate déshydrogénase. La coloration au bleu trypan et la contamination d'érythrocytes était toujours inférieure à 0,1% et la fuite de lactate déshydrogénase est demeurée inférieure à 1% à 25°C pendant 10 h. La charge énergétique dans des cellules fraîchement isolées se situait entre 0,65 et 0,74. L'alanine (10 mM) a produit des taux plus élevés de gluconéogenèse et d'oxydation que le lactate, soit $3,17 \pm 0,65$ $\mu\text{mol glucose}/(\text{g hématocrite} \cdot \text{h})$ et $9,1 \pm 1,19$ $\mu\text{mol CO}_2/(\text{g} \cdot \text{h})$, alors que ces taux étaient de $0,47 \pm 0,08$ et de $1,8 \pm 0,27$ en présence de lactate. La phosphoenolpyruvate carboxykinase s'est avérée à 30% d'origine cytosolique et à 70% d'origine mitochondriale, ce qui est normal étant donné la capacité du foie d'utiliser à la fois la lactate et l'alanine comme substrats au cours de la gluconéogenèse. Si la gluconéogenèse constituait la principale voie d'élimination du lactate après l'exercice, la récupération durerait 3800 h. Le foie ne constitue donc pas le principal siège de la néosynthèse du glucose et de la clearance du lactate après un épisode d'exercice intense chez les thons.

[Traduit par la rédaction]

Introduction

Tuna are able to swim at 3–5 body lengths/s for prolonged time periods, and for short (1 min) bursts they can achieve speeds of up to 20 body lengths/s (Waters and Fierstine 1964). Burst swimming involves a powerful glycolytic activation leading to lactate accumulation in white muscle of nearly 100 $\mu\text{mol/g}$ (Guppy et al. 1979). More recently, Arthur et al. (1992) measured even higher lactate concentrations in tuna white muscle. Under these conditions, blood lactate concentrations rise to values approaching 50 mM (Guppy et al. 1979; Weber et al. 1986; Arthur et al. 1992). What is the fate of this large lactate load?

The classical picture of postexercise lactate clearance emphasizes two main fates: either (i) the lactate is oxidized at various sites in the body or (ii) it is reconverted to glucose and glycogen via liver gluconeogenesis. Glucose formed this way serves ultimately as the precursor for muscle glycogen. This inter-tissue cycling of carbon (glycogen-derived muscle lactate to

liver glucose; liver glucose back to muscle glycogen) is termed the Cori cycle. In most teleosts thus far studied, the Cori cycle is not considered to contribute significantly to postexercise lactate clearance; the capacity of the liver gluconeogenic arm of the Cori cycle is simply insufficient to account for much lactate clearance. Instead, most (and maybe all) muscle glycogen resynthesis seems to take place in situ from the lactate formed in the preceding exercise period (Weber et al. 1986; Milligan and McDonald 1988; Schulte et al. 1992; Moyes et al. 1992). Since tuna may maintain high body temperatures and have higher than usual enzymatic activities (see Guppy et al. 1979), we considered the possibility that in this species the Cori cycle could be more important in lactate clearance than in other teleosts. For this reason, we attempted to evaluate liver gluconeogenic capacities directly by studying isolated tuna hepatocytes.

Specifically, our goal was to determine the relative capacities of gluconeogenesis from the amino acid alanine and from

lactate, based on [^{14}C]substrate flux and the intracellular distribution of phosphoenolpyruvate carboxykinase (PEPCK).

Materials and methods

Experimental animals

Skipjack tuna, *Katsuwonus pelamis*, were caught by hook and line by local fishermen and transported to the Kewalo Research Facility (National Marine Fisheries Service, Honolulu Laboratory). The fish were quickly transferred from bait wells to large, well-aerated circulating saltwater holding tanks at 25°C. Fish were maintained for up to 4 days without feeding under the above conditions and were generally used on the 2nd and 3rd days.

Hepatocytes isolation

Fish weighing between 1.5 and 3 kg were rapidly netted and killed by a sharp blow to the head. An incision was made ventrally from the anus to the pectoral girdle to expose the liver. The liver was removed and the hepatic portal vein quickly cannulated. The liver was perfused at 4 mL/min for 10 min with solution A, consisting of 196 mM NaCl, 4 mM KCl, 0.9 mM NaH_2PO_4 , 10 mM sodium HEPES (*N*-[2-hydroxyethyl]piperazine-*N'*-[2-ethanesulfonic acid]), and 10 mM NaHCO_3 at pH 7.2 and 25°C. It was then perfused for another 10 min with solution B (solution A with 129 U/mL collagenase, Sigma Lot 39F6804). The composition of the perfusion media was determined from the blood osmolite profiles of Bourke et al. (1987). All solutions were prebubbled with 99% O_2 and 1% CO_2 . Following perfusion the digested liver was placed in ice-cold solution A and gently teased apart with two razor blades. The resultant cell slurry was poured first through a 273- μm nylon screen and then through a 75- μm screen to remove large fragments. Cells were washed and concentrated by centrifuging at $130 \times g$ for 4 min in a bench-top clinical centrifuge fitted with a swing-out bucket rotor head and placed in a 4°C refrigerator. The cells were resuspended in solution C (solution A with 2% bovine serum albumin (BSA), 4 mM CaCl_2 , and 0.8 mM MgSO_4) and centrifuged a second time. Finally the cells were adjusted to 60–100 mg/mL or approximately 2.2×10^7 cells/mL and allowed to stand on ice for 2 h before use. Cells were counted in a Neubauer hemocytometer and weighed by centrifuging a known volume in a preweighed 1.5 mL centrifuge tube at $15\,000 \times g$ for 10 min in an Eppendorf Model 5414 bench-top centrifuge, then decanting and wiping out excess liquid with a Kimwipe tissue and reweighing. Red blood cell (RBC) contamination and trypan blue staining were determined by incubating hepatocytes with 0.02% (w/v) trypan blue and counting them in a Neubauer chamber. Yield was not rigorously determined but was estimated to be greater than 50%. Lactate dehydrogenase (LDH) leakage was measured by centrifuging a 1-mL aliquot of cells at $100 \times g$ for 10 min in a clinical centrifuge (as above) and removing an aliquot of supernatant for an LDH assay. The pelleted cells were resuspended in 25 mM imidazole buffer containing 2 mM ethylenediaminetetraacetic acid (EDTA) and 0.5% Triton X-100 at pH 7 and sonicated twice for 10 s each time at a medium setting. An aliquot was then assayed for LDH activity.

To assess energy charge (EC, Atkinson 1977) an aliquot of cells was extracted with perchloric acid (PCA, final concentration 7%), centrifuged, and neutralized with 3 M K_2CO_3 . Following centrifugation to remove precipitated KClO_4 , a volume was taken for ATP, ADP, and AMP measurement by an LKB 2152 high-performance liquid chromatograph fitted with a 7- μm Aquapore AX-300 weak ion exchange column (Brownlee Labs), using a procedure described by Schulte et al. (1992).

Glucoseogenic rate determination

The rate of gluconeogenesis from radiolabelled precursors by isolated hepatocytes has been previously described (French et al. 1981), and the experiments described here were conducted in the same fashion. The incubations were carried out at 25°C with 10 mM substrate and 0.2 μCi (1 Ci = 37 GBq) of [^{14}C]substrate for intervals of up to 3 h. Radiolabelled samples were counted in a Packard Tri-Carb 4640 liquid scintillation counter.

Total enzyme activity and compartmentation

Two 0.5-g liver samples were obtained in less than a minute after capture, wiped dry with a paper towel, and weighed. The known weight of tissue was quickly immersed in 5 vol. ice-cold homogenization medium (25 mM Tris HCl, 2 mM EDTA, and 0.5% Triton X-100, pH 7.5, solution D) and homogenized with an Ultra-Turrax homogenizer by being ground 2 times for 10 s each and then sonicated 2 times for 10 s each. Homogenates were pipetted into 1.5-mL centrifuge tubes and centrifuged for 10 min at $15\,000 \times g$. A portion of the supernatant was taken for assay immediately, while another was frozen in liquid N_2 and stored on dry ice. The second sample was placed in 5 vol. ice-cold 250 mM sucrose, 2 mM EDTA, and 20 mM HEPES buffer at pH 7.2. The tissue was minced with the tip of a fine pair of scissors and homogenized for 10–15 s with an Ultra-Turrax homogenizer at a medium setting. The homogenate was centrifuged in a refrigerated bench-top Jouan (MR 14.11) centrifuge for 10 min at $300 \times g$ to remove large cellular debris (discarded). The supernatant was then centrifuged for another 10 min at $8000 \times g$ to bring down the mitochondria. The supernatant from the last centrifugation was decanted and assayed immediately for PEPCK, citrate synthase (CS), LDH, malate dehydrogenase (MDH), and glutamate dehydrogenase (GPT) activities. The pellet was resuspended in homogenization buffer (solution D), sonicated 2 times for 10 s each, centrifuged, and assayed for the same enzyme activities. The relative amounts of CS found in the cytosol and LDH found in the matrix could be used to correct for contamination of either compartment.

Enzymes were assayed using a Perkin–Elmer Lambda 2 spectrophotometer and data collected via an IBM computer loaded with a Perkin–Elmer computerized spectroscopy software program (PECSS version 3.2). All assays were tested for saturating substrate concentrations and coupling enzyme activities. Coupling enzymes shipped as precipitates in ammonium sulphate were centrifuged for 1 min at $15\,000 \times g$ and resuspended in assay buffer. The following enzymes were assayed in 50 mM imidazole, pH 7, at 25°C. LDH: 1 mM pyruvate (omitted for control), 0.2 mM NADH. MDH: 10 mM oxaloacetate (omitted for control), 0.15 mM NADH. GPT: 200 mM alanine (omitted for control), 10 mM α -ketoglutarate, 0.025 mM pyridoxal 5-phosphate, 0.15 mM NADH, excess LDH. PEPCK was assayed in 50 mM Tris HCl, 20 mM NaHCO_3 , and 1 mM MnCl_2 (from 50 mM stock solution), pH 7.5, at 25°C (Petrescu et al. 1979), with the addition of the following: 0.5 mM phosphoenolpyruvate, 0.2 mM deoxyguanosine 5'-diphosphate (omitted for control), 0.1 mM NADH, and excess MDH. CS was assayed in 50 mM Tris HCl, pH 8.0, at 25°C, with the addition of the following: 0.3 mM acetyl-CoA, 0.5 mM oxalacetate (omitted for control), and 0.1 mM dithio-bis(nitrobenzoic acid).

Chemicals, enzymes, and radioisotopes

Uniformly labelled [^{14}C]lactate and alanine were obtained from ICN Biomedicals, Inc. (California). Radioisotopes were dried under a stream of N_2 and dissolved in Solution C (without BSA) and used immediately. Amyloglucosidase and acetyl-CoA were obtained from Boehringer Mannheim, Canada, Inc. (Laval). All other chemicals and enzymes were purchased from Sigma Chemical Co. (St. Louis).

Results

In a group of animals separate from those for hepatocyte isolation the proportion of liver to total body weight was determined to be 1.8% ($n = 4$).

RBC contamination and trypan blue staining were less than 0.1% in all experimental preparations. The supernatant of freshly isolated cells always had less than 0.5% of the LDH activity ($n = 5$) and after a 10-h incubation at 25°C, LDH leakage was less than 1% ($n = 2$). The EC of freshly isolated cells used in gluconeogenic experiments ranged from 0.65 to 0.75.

A comparison of the rates of gluconeogenesis from alanine

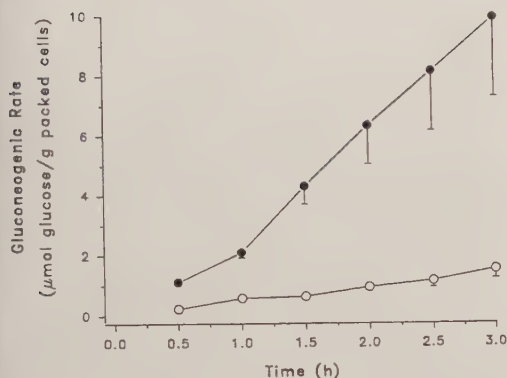


FIG. 1. Gluconeogenic rates obtained from tuna hepatocytes incubated in the presence of 10 mM alanine (●) or 10 mM lactate (○) over a 3-h time course. Each curve represents the mean $\pm$ standard error of 4 (alanine) and 5 (lactate) animals; in some cases the symbol covers the standard error bar.

and lactate over a 3-h time course is shown in Fig. 1. For both substrates the rate of gluconeogenesis became linear after 1 h of incubation. The rate of gluconeogenesis from alanine was approximately 7 times greater than from lactate: 3.17 ± 0.65 and 0.47 ± 0.08 $\mu\text{mol glucose}/(\text{g wet weight packed cells} \cdot \text{h})$, respectively. A similar relationship held for the oxidation of these substrates; however, the rate was linear throughout the 3-h time course, and alanine was oxidized at a rate 5 times that of lactate: 9.1 ± 1.2 and 1.8 ± 0.27 $\mu\text{mol CO}_2/(\text{g wet weight packed cells} \cdot \text{h})$, respectively ($n = 5$ in both cases, data not shown). The oxidative rates obtained from uniformly labelled substrates can only be qualitatively interpreted due to the possible randomization of label.

The intracellular localization of PEPCK was estimated and is shown in Table 1. The activities of the two marker enzymes, CS and LDH, in the two compartments demonstrate a clean separation of matrix from cytosol, with the cytosol being contaminated by only 6% CS activity and the matrix space by only 11% of the total LDH activity. PEPCK was found in both compartments, approximately 70% mitochondrial and 30% cytosolic (corrected for contamination from the respective compartments), or 5.7 and 3 units/g of tissue (Table 1), respectively. This represents 190 times more activity in the cytosol and 360 times more activity in the intramitochondrial space than required by the measured gluconeogenic rates. LDH, the first enzyme in gluconeogenesis from lactate, has a total activity of 26 units/g wet weight tissue. MDH and GPT, two necessary enzymes in the gluconeogenic pathway from alanine, have total activities of 992 and 75 units/g wet weight, respectively. Most of the MDH activity is located in the cytosol (87%), whereas GPT was determined to be 94% cytosolic.

Discussion

On the basis of the viability criterion employed, the hepatocyte preparation could be considered a healthy one. LDH leakage occurred at a very low rate, RBC contamination and trypan blue staining were minimal, and a high EC of 0.65–0.74 was observed. Atkinson (1977) points out that an EC less

TABLE 1. Total enzyme activities and compartmentation of PEPCK, MDH, GPT, and the marker enzymes, CS and LDH, in tuna liver

	Mitochondrial activity (%)	Total activity*
PEPCK	65 (4)	8.7 ± 1.3 (7)
CS	95 (5)	8.7 ± 1.2 (7)
LDH	11 (5)	25.8 ± 2.2 (7)
MDH	13 (2)	991.9 ± 179.0 (7)
GPT	6 (2)	74.6 ± 21.5 (6)

NOTE: Values are given as means $\pm$ standard error, with the number of animals used in parentheses.

*Enzyme activities were measured at 25°C and are given as $\mu\text{mol}/(\text{min} \cdot \text{g wet tissue weight})$.

than this results in cell death. The cells were also shown to be gluconeogenic. This is a complex two-compartment pathway and clearly demonstrates the metabolic competence of the hepatocytes. Moreover, the oxidation of alanine and lactate emphasizes the competence of the mitochondrial compartment. Taken together, these data suggest that the hepatocyte preparations were metabolically competent.

In Fig. 1 the rate of gluconeogenesis is shown to become linear after 1 h of incubation. The highest rates of gluconeogenesis and oxidation were obtained from alanine. Interestingly, the rates are similar to those found in trout, but the fuel preference is reversed. That is, the gluconeogenic rate from 10 mM lactate in the trout is approximately 4.2 $\mu\text{mol glucose}/(\text{g} \cdot \text{h})$ (corrected for temperature, French et al. 1981) whereas in the tuna it is 0.47 $\mu\text{mol glucose}/(\text{g} \cdot \text{h})$. In contrast, 10 mM alanine supports a rate of 3.17 $\mu\text{mol}/(\text{g} \cdot \text{h})$ in the tuna and only 0.24 $\mu\text{mol}/(\text{g} \cdot \text{h})$ in the trout. All of these gluconeogenic values are very much lower than those measured in the rat, in which the rates from alanine and lactate have been measured to be 64 and 107 $\mu\text{mol glucose}/(\text{g} \cdot \text{h})$ at 25°C, respectively (Elliott et al. 1976). Interestingly, the approximately 10-fold difference in gluconeogenic rates from lactate between the trout and tuna coincides with a 10-fold difference in liver LDH, the trout having 251 U/g (Mommensen 1986). Although LDH is usually thought to be a near-equilibrium reaction *in vivo*, it is possible that the combined effects of pH and substrate concentrations may limit its activity in the required direction in tuna liver gluconeogenesis.

Based on the gluconeogenic rate from lactate (above) one can calculate the length of time required to clear a bolus of lactate generated by the white muscle mass of a tuna. In a 2-kg tuna the white muscle mass is estimated to be 1.3 kg (approximately two-thirds of body weight, Graham and Diener 1978) and the liver comprises 1.8% of the body weight, or 0.036 kg. Lactate concentrations in white muscle have been measured to be as high as 100 $\mu\text{mol/g}$ (Guppy et al. 1979) and would therefore generate 130 mmol lactate. At the measured maximum gluconeogenic rate the liver would require 3800 h to clear the lactate produced by the white muscle! Tuna white muscle has been shown to reduce lactate concentrations to preexercise levels in approximately 2 h (Arthur et al. 1992). This suggests that Cori cycle activity accounts for less than 34 $\mu\text{mol glycosyl equivalents}$, making it an insignificant route for postexercise glycogen repletion and lactate clearance in tuna as in other teleosts.

The intracellular distribution of PEPCK (Table 1) is consistent with the hypothesis that alanine is a good gluconeogenic

substrate. Interestingly, gluconeogenesis from lactate is consistently greater than the alanine rate in most other teleost fishes investigated (for review see Suarez and Mommsen 1987). When the rates of gluconeogenesis measured in other teleosts are considered, the tuna liver is not unusual in its capacity to deal with lactate loads, but the tuna is unusual in its ability to generate high lactate loads in white muscle. The metabolic arrangement in tuna may represent a specialization to rapidly convert dietary protein to glucose.

In summary, viable skipjack tuna hepatocytes were prepared, and greater rates of gluconeogenesis were obtained from alanine than from lactate. The distribution of PEPCK in both the cytosolic and matrix compartments is consistent with the liver's ability to use both amino acids and lactate as gluconeogenic substrates. The maximum rate of gluconeogenesis is not sufficient to implicate the liver as a significant participant in white muscle recovery, but it does suggest that tuna liver plays a more important role in synthesizing glucose from dietary amino acids than from lactate generated in burst exercise.

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Oxygen transport and cardiovascular responses in skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) exposed to acute hypoxia

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Summary. Responses to acute hypoxia were measured in skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) (≈ 1 –3 kg body weight). Fish were prevented from making swimming movements by a spinal injection of lidocaine and were placed in front of a seawater delivery pipe to provide ram ventilation of the gills. Fish could set their own ventilation volumes by adjusting mouth gape. Heart rate, dorsal and ventral aortic blood pressures, and cardiac output were continuously monitored during normoxia (inhalant water $PO_2 > 150$ mmHg) and three levels of hypoxia (inhalant water $PO_2 \approx 130$, 90, and 50 mmHg). Water and blood samples were taken for oxygen measurements in fluids afferent and efferent to the gills. From these data, various measures of the effectiveness of oxygen transfer, and branchial and systemic vascular resistance were calculated. Despite high ventilation volumes (4 – $71 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$), tunas extract approximately 50% of the oxygen from the inhalant water, in part because high cardiac outputs (115 – $132 \text{ ml} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) result in ventilation/perfusion conductance ratios (0.75 – 1.1) close to the theoretically ideal value of 1.0. Therefore, tunas have oxygen transfer factors

($\text{ml O}_2 \cdot \text{min}^{-1} \cdot \text{mmHg}^{-1} \cdot \text{kg}^{-1}$) that are 10–50 times greater than those of other fishes. The efficiency of oxygen transfer from water in tunas ($\approx 65\%$) matches that measured in teleosts with ventilation volumes an order of magnitude lower. The high oxygen transfer factors of tunas are made possible, in part, by a large gill surface area; however, this appears to carry a considerable osmoregulatory cost as the metabolic rate of gills may account for up to 70% of the total metabolism in spinally blocked (i.e., non-swimming) fish. During hypoxia, skipjack and yellowfin tunas show a decrease in heart rate and increase in ventilation volume, as do other teleosts. However, in tunas hypoxic bradycardia is not accompanied by equivalent increases in stroke volume, and cardiac output falls as HR decreases. In both tuna species, oxygen consumption eventually must be maintained by drawing on substantial venous oxygen reserves. This occurs at a higher inhalant water PO_2 (between 130 and 90 mmHg) in skipjack tuna than in yellowfin tuna (between 90 and 50 mmHg). The need to draw on venous oxygen reserves would make it difficult to meet the oxygen demand of increasing swimming speed, which is a common response to hypoxia in both species. Because yellowfin tuna can maintain oxygen consumption at a seawater oxygen tension of 90 mmHg without drawing on venous oxygen reserves, they could probably survive for extended periods at this level of hypoxia.

Key words: Hypoxia – Cardiovascular – Oxygen transport – Skipjack tuna *Katsuwonus pelamis* – Yellowfin tuna, *Thunnus albacares*

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Abbreviations: BP_{da}, BP_{va} dorsal, ventral aortic blood pressure; C_aO₂, C_vO₂ oxygen content of arterial, venous blood; D_{O2} diffusion capacity; E_b, E_w effectiveness of O₂ uptake by blood, and from water, respectively; Hct hematocrit; HR heart rate; PCO₂ carbon dioxide tension; P_aCO₂, P_vCO₂ carbon dioxide tension of arterial and venous blood, respectively; PO₂ oxygen tension; P_aO₂, P_vO₂, P_iO₂, P_eO₂ oxygen tension of arterial blood, venous blood, and inspired and expired water, respectively; pH_a, pH_v pH of arterial and venous blood, respectively; P_w–_b effective water to blood oxygen partial pressure difference; ΔP_g partial pressure (tension) gradient; $\dot{Q}$ cardiac output; R vascular resistance; SV stroke volume; SEM standard error of mean; TO₂ transfer factor; U utilization; $\dot{V}_g$ ventilation volume; $\dot{V}_{O_2}$ oxygen consumption

Introduction

Anatomical, physiological, and biochemical adaptations enable tunas to consume oxygen at rates that are unmatched by other teleosts (Brett 1972; Gooding et al. 1981; Brill 1987). As a consequence of their high aerobic

demand even at low swimming speeds (Gooding et al. 1981; Jones et al. 1990), the distribution of tunas has been hypothesized to be determined in large measure by ambient oxygen levels (Barkley et al. 1978; Sund et al. 1981). Early laboratory and field studies on the hypoxia sensitivity of tunas have focused on changes in swimming speed (Dizon 1977), time to mortality (Gooding et al. 1981), or fisheries catch data (Ingham et al. 1977; Hanamoto 1987). Results from these studies suggest that hypoxia tolerance is quite variable among tuna species (Sharp 1978).

More recent work investigating the ambient oxygen sensitivity of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) (Bushnell et al. 1990; Bushnell and Brill 1991a) indicates that both species respond to hypoxia by increasing gape, $\dot{V}_g$ and swimming speed, while reducing HR and ultimately $\dot{Q}$. Based on when cardiorespiratory responses are initiated (P_{iO_2} 110–139 mmHg), Bushnell et al. (1990) have demonstrated that tunas are no more sensitive to hypoxia than other marine fishes. Although the observed physiological and behavioral changes could be presumed to be aimed at maintaining oxygen supply to the tissues, none of the previous studies have demonstrated how effective they are in achieving this. Also, no previous studies have measured the effects of hypoxia on arterial or venous blood pressures, blood gases, or blood acid-base status in tunas.

The primary objectives of this study were to determine how well the cardiorespiratory systems of skipjack and yellowfin tunas function in normoxia compared with other fish species, and how well they are able to maintain oxygen delivery to the tissues during hypoxia. To meet these objectives, HR, $\dot{Q}$, P_{iO_2} , P_{eO_2} and P_{aO_2} , P_{vO_2} , C_{iO_2} and C_{vO_2} were measured. When combined in appropriate equations with estimates of $\dot{V}_g$, these variables are used to calculate standard measures of performance of the cardiorespiratory system in normoxia and hypoxia.

Materials and methods

Ten yellowfin tuna (1.42 ± 0.2 kg) and nine skipjack tuna (1.64 ± 0.3 kg) were used. Fish were captured by local commercial fishermen and maintained in shore-side tanks at the Kewalo Research Facility (Southwest Fisheries Science Center Honolulu Laboratory, National Marine Fisheries Service, NOAA). Fish maintenance and handling procedures at this laboratory are described in Nakamura (1972). Food was presented daily, but withheld for 24 h prior to an experiment to allow sufficient time for gut clearance (Magnuson 1969).

Surgical and instrumentation procedures. Fish were netted in their holding tank and anesthetized by being placed in a plastic bag containing oxygenated seawater and MS222 ($1 \text{ g} \cdot \text{l}^{-1}$) buffered with an equimolar concentration of NaHCO_3 . Fish were then quickly moved to a surgery table where they were force-ventilated with oxygenated seawater containing a maintenance dose of NaHCO_3 -buffered MS222 ($0.1 \text{ g} \cdot \text{l}^{-1}$). Subjects were instrumented with a pulsed Doppler cardiac output probe, four exhalant water sampling catheters, and dorsal and ventral aorta cannulae as de-

scribed in Jones et al. (1986, 1990), Bushnell et al. (1990), and Bushnell and Brill (1991a).

Following surgery, which generally took 50–60 min, fish were spinally blocked with an injection of lidocaine HCl and placed ventral side up in a restraining apparatus described in Bushnell et al. (1990). They were then positioned immediately in front of a pipe delivering seawater at approximately $351 \cdot \text{min}^{-1}$. Tunas are obligate ram ventilators, and this system provides adequate ventilation while allowing fish to set their own $\dot{V}_g$ (Bushnell et al. 1990). Fish were left undisturbed for at least 1 h after the completion of surgery to recover from anesthesia.

Measurement and data recording procedures. The analyses of water PO_2 , blood gases, and blood oxygen content were performed using three Radiometer PHM 73 blood gas analyzers. The first was connected to an oxygen probe mounted in a water-jacketed, flow-through cuvette. Cuvette temperature was maintained at 25°C . The oxygen probe, calibrated with standard zero- PO_2 solution and air-saturated seawater, was used to measure P_{iO_2} and P_{eO_2} . A second blood gas analyzer was connected to a BMS3/MK2 Blood Micro System (also maintained at 25°C) and was used to measure pH, PO_2 , and PCO_2 of dorsal aorta (arterial) and ventral aorta (venous) blood samples (pHa, pHv, P_{aO_2} , P_{vO_2} , P_{aCO_2} , and P_{vCO_2} , respectively). The PO_2 electrode was calibrated with zero PO_2 solution and air-saturated saline, the PCO_2 electrode with precision-mixed gases (PCO_2 4.0 and 23.6 mmHg), and the pH electrode with pH 7.00 and 7.80 buffers. The third blood gas analyzer was used to measure blood oxygen content as described by Tucker (1967).

A Valpey-Fischer¹ Model VF-1 pulsed Doppler system was used to measure $\dot{Q}$ [theory of operation described in Hartley et al. (1978)]. A single naked crystal (1 mm diameter) was embedded in a drop of silicon rubber sealant which was trimmed to a smooth oval shape ($0.5 \text{ cm} \times 0.75 \text{ cm}$). The embedded crystal was glued with Vetbond tissue adhesive to the thin membrane in the gill cavity overlying the ventral aorta as described in Bushnell et al. (1990).

The mean $\dot{Q}$ signal from the Doppler flow system was calibrated immediately following the 1 h allowed for recovery from surgery and anesthesia by simultaneous measurement of $\dot{Q}$ using dye dilution. Indocyanine green dye solution ($0.1\text{--}0.2 \text{ ml}$, $\approx 2 \text{ mg} \cdot \text{ml}^{-1}$) was injected into the ventral aorta via the indwelling cannula. Concentration of the dye in blood downstream of the heart was determined by withdrawing a subsample of dorsal aortic blood through a densitometer cuvette connected to a Waters D-400 Densitometer. Data recording and calculation of $\dot{Q}$ from dye dilution curves were performed using standard procedures as described in Bushnell (1988) and Brill and Bushnell (1989). Five to seven measurements of $\dot{Q}$, with 5-min intervals between each, were made on every fish.

BP_{da} and BP_{va} were monitored with U-Onics P-106 Physiological Pressure Transducers connected to Gould amplifiers. The transducers were calibrated daily with a water manometer. In most cases, the BP_{va} signal triggered a cardiograph. The output signals from pressure transducers, the Radiometer measuring P_{iO_2} , the pulsed Doppler flow meter (mean and pulsatile $\dot{Q}$), and cardiograph were simultaneously recorded on a Gould 260 6-channel pen recorder. In addition, a Dianachart A/D converter and an IBM AT computer recorded mean BP_{va} and BP_{da} , $\dot{Q}$, HR, and P_{iO_2} every 5 s. These data were stored on disk for later analysis. Data presented here were taken from the digitized records with their accuracy checked against the chart records.

No attempt was made to measure $\dot{V}_g$ in this study, because preliminary experiments had shown that having both the dye diffuser and the dorsal aorta catheter in the mouth would interfere with ventilatory water flow. $\dot{V}_g$ was therefore estimated from regression equations of $\dot{V}_g$ on P_{iO_2} based on data obtained previously under similar circumstances (Bushnell 1988; Bushnell et al. 1990).

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

For yellowfin and skipjack tunas, respectively, the regression equations used were:

$$\dot{V}_g = \left(\frac{P_iO_2 - 154}{154} \right) \cdot (-7.16) + 3.9; \quad r^2 = 0.92 \quad (1)$$

$$\text{and } \dot{V}_g = \left(\frac{P_iO_2 - 154}{154} \right) \cdot (-5.67) + 6.7; \quad r^2 = 0.98 \quad (2)$$

where $\dot{V}_g$ is in $l \cdot \min^{-1} \cdot \text{kg}^{-1}$ and P_iO_2 in mmHg.

Experimental protocol. Fish were exposed to three levels of hypoxia ($P_iO_2 \approx 130, 90$, and 50 mmHg), presented in random order. Control measurements of cardiorespiratory variables were made during the normoxic period ($P_iO_2 > 150$ mmHg) immediately preceding the hypoxic episode. HR, BP_{ves}, BP_{des}, $\dot{Q}$, and P_iO_2 were continuously recorded, exhalant water samples were taken (for P_eO_2) and stored in 5-ml plastic syringes, and dorsal and ventral aortic blood samples taken in pre-cooled glass syringes and stored on ice. P_iO_2 was then reduced to the preselected level and held there for 2 min before the second series of blood and exhalant water samples were taken. The P_iO_2 was then returned to normoxic levels and the fish left undisturbed for 1 h. During this time, the eight water and four blood samples were analyzed. Hct was also determined.

At the conclusion of the experiment, fish were sacrificed, weighed, and necropsied to record the position of the dorsal and ventral aortic catheters and the pulsed Doppler blood flow probe.

Calculations. The Fick principle was used to calculate the following three metabolic rates:

Whole animal $\dot{V}O_2$ ($= \dot{V}O_2\text{-total}$) in $\text{ml } O_2 \cdot \min^{-1} \cdot \text{kg}^{-1}$;

$$\dot{V}O_2\text{-total} = \dot{V}_g \cdot ((P_iO_2 - P_eO_2) \cdot \alpha_w) \quad (3)$$

where α_w = solubility coefficient of oxygen in seawater ($\text{ml } O_2 \cdot l^{-1} \cdot \text{mmHg}^{-1}$) at 25°C ;
 $\dot{V}O_2$ of all tissues excluding the gills ($= \dot{V}O_2\text{-body}$) in $\text{ml } O_2 \cdot \min^{-1} \cdot \text{kg}^{-1}$;

$$\dot{V}O_2\text{-body} = \dot{Q} \cdot \left(\frac{C_aO_2 - C_vO_2}{100} \right) \quad (4)$$

where $\dot{Q}$ is in $\text{ml} \cdot \min^{-1} \cdot \text{kg}^{-1}$, and C_aO_2 and C_vO_2 are in $\text{ml } O_2 \cdot \text{dl}^{-1}$;
and $\dot{V}O_2$ of the gills ($= \dot{V}O_2\text{-gill}$) in $\text{ml } O_2 \cdot \min^{-1} \cdot \text{kg}^{-1}$

$$\dot{V}O_2\text{-gill} = (\dot{V}O_2\text{-total} - \dot{V}O_2\text{-body}) \quad (5)$$

Data from other measured variables were used to calculate the following standard indicators of cardiorespiratory function:
Oxygen delivery to all tissues excluding the gills (O_2 delivery, in $\text{ml } O_2 \cdot \min^{-1} \cdot \text{kg}^{-1}$);

$$O_2 \text{ delivery} = \dot{Q} \cdot (C_aO_2 \cdot 100) \quad (6)$$

Ventilation/perfusion conductance ratio ($\dot{V}_g/\dot{Q}$ conductance);

$$\frac{\dot{V}_g}{\dot{Q}} \text{ conductance} = \frac{\dot{V}_g \cdot \alpha_w}{\dot{Q} \cdot \alpha_b} \quad (7)$$

where α_b is the solubility coefficient of blood at the prevailing P_aO_2 (i.e., C_aO_2/P_aO_2);
Utilization (U , %) or the fraction of oxygen content removed from the water;

$$U = \left(\frac{P_iO_2 - P_eO_2}{P_iO_2} \right) \cdot 100 \quad (8)$$

E_w (%), which is the ratio of the actual rate of removal of oxygen from the water ($\dot{V}O_2$) and the theoretical maximum rate possible (Hughes and Shelton 1962);

$$E_w = \left(\frac{P_iO_2 - P_eO_2}{P_iO_2 - P_vO_2} \right) \cdot 100 \quad (9)$$

Effectiveness of oxygen uptake by blood (E_b , %) which is the ratio of the actual rate of oxygen uptake by the blood and the theoretical maximum rate possible;

$$E_b = \left(\frac{C_aO_2 - C_vO_2}{C_{ia}O_2 - C_vO_2} \right) \cdot 100 \quad (10)$$

where $C_{ia}O_2$ is the oxygen content that would be achieved if P_aO_2 was equal to P_iO_2 ;

Transfer factor (TO_2 , in $\text{ml } O_2 \cdot \min^{-1} \cdot \text{mmHg}^{-1} \cdot \text{kg}^{-1}$) which is the rate of O_2 transfer from the water to the blood per unit partial pressure difference (ΔP_g) between P_iO_2 and P_vO_2 (Randall et al. 1967; Piiper and Scheid 1984);

$$TO_2 = \frac{\dot{V}O_2\text{-water}}{\Delta P_g} \quad (11)$$

where

$$\Delta P_g = \frac{1}{2} \cdot (P_iO_2 + P_vO_2) - \frac{1}{2} \cdot (P_aO_2 + P_vO_2) \quad (12)$$

This calculation assumes a linear dissociation curve, and its use has been criticized by Piiper and Baumgarten-Schumann (1968). Therefore, we also calculated diffusion capacity (DO_2 , in $\text{ml } O_2 \cdot \min^{-1} \cdot \text{mmHg}^{-1} \cdot \text{kg}^{-1}$) which is similar to TO_2 but accommodates the properties of hemoglobin (Scheid and Piiper 1976)

$$DO_2 = \frac{\dot{V}O_2\text{-total}}{P_w - b} \quad (13)$$

where

$$P_w - b = \frac{(P_iO_2 - P_vO_2) - (P_aO_2 - P_vO_2)}{\ln \left[\frac{(P_iO_2 - P_vO_2)}{(P_aO_2 - P_vO_2)} \right]} \quad (14)$$

$^2C_{ia}O_2$ was calculated based on the yellowfin and skipjack tuna blood oxygen dissociation curves presented in Fig. 1 [data from Brill and Bushnell (1991)]. Regression lines were fitted to these data using an iterative least-squares technique (Sigmaplot ver. 4.1) and the following non-linear equation

$$\text{Saturation (\%)} = \frac{a - d}{\left[1 + \left(\frac{PO_2}{c} \right)^b \right]^e} + d$$

The fitted parameters from skipjack tuna blood were:

$a = 101.93887$, $b = -1.45585$, $c = 8.15136$, $d = -1.80961$, and $e = 3.41219$

and for yellowfin tuna blood were:

$a = 103.40217$, $b = -3.29641$, $c = 44.91710$, $d = 1.10164$, and $e = 0.27497$.

Percent saturation at a given P_aO_2 was calculated from these equations and maximum blood oxygen content estimated by extrapolating to 100% saturation from measured C_aO_2 . Percent saturation at a given P_iO_2 was then calculated and $C_{ia}O_2$ estimated based this value and maximum blood oxygen content.

Data from measured variables were also used to calculate the following standard indicators of cardiovascular function:

SV (in $\text{ml} \cdot \text{beat}^{-1} \cdot \text{kg}^{-1}$);

$$\text{SV} = \frac{\dot{Q}}{\text{HR}} \quad (15)$$

Resistance to blood flow offered by the gills (R_{branch} , in $\text{mmHg} \cdot \text{ml}^{-1} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$);

$$R_{\text{branch}} = \frac{\text{BP}_{\text{va}} - \text{BP}_{\text{da}}}{\dot{Q}} \quad (16)$$

Resistance to blood flow offered by the systemic circulation (R_{system} , in $\text{mmHg} \cdot \text{ml}^{-1} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$);

$$R_{\text{system}} = \frac{\text{BP}_{\text{da}} - \text{BP}_{\text{v}}}{\dot{Q}} \quad (17)$$

Total resistance to blood flow offered by the gill and systemic circulations (R_{total} , in $\text{mmHg} \cdot \text{ml}^{-1} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$);

$$R_{\text{total}} = \frac{\text{BP}_{\text{va}} - \text{BP}_{\text{v}}}{\dot{Q}} \quad (18)$$

where venous pressure (BP_{v}) is assumed to be zero in both cases; Cardiac power output ($\text{mW} \cdot \text{kg}^{-1}$);

$$\text{cardiac power output} = (\text{BP}_{\text{va}} \cdot \dot{Q}) \cdot 2.23 \cdot 10^{-3} \quad (19)$$

where $2.23 \cdot 10^{-3}$ converts $\text{mmHg} \cdot \text{ml} \cdot \text{min}^{-1}$ to mW .

Statistical analysis procedures. As stated, experiments consisted of three hypoxia trials during which fish were exposed to P_{O_2} s of approximately 130 mmHg, 90 mmHg, or 50 mmHg. Changes occurring during hypoxia were calculated by comparing values measured during the normoxic period (1–3 min) immediately preceding a hypoxic episode with those measured during the hypoxic episode. The 95% confidence intervals were used to determine statistically significant changes occurring during hypoxia. Inter-trial comparison of variables in the three control or hypoxia groups, as well as comparisons with data collected in previous studies, were made using analysis of variance (ANOVA) and a multiple-range test. Interspecific comparisons, or comparisons of data collected in only one other study, were made with an unpaired Student's *t*-test. In all

Table 1. Mean values ($\pm$ SEM) of cardiorespiratory variables measured in normoxia and significant changes occurring during hypoxia in yellowfin tuna (*Thunnus albacares*)

Variable	Control	Hypoxia		
		($P_{\text{O}_2} \approx 130$ mmHg)	($P_{\text{O}_2} \approx 90$ mmHg)	($P_{\text{O}_2} \approx 50$ mmHg)
P_{O_2} (mmHg)	154.1 $\pm$ 0.6 (10)	-23.6 $\pm$ 1.8 (8)	-65.5 $\pm$ 2.2 (10)	-103.1 $\pm$ 1.9 (7)
P_{aO_2} (mmHg)	75.9 $\pm$ 3.7 (10)	NS	-16.8 $\pm$ 4.4 (10)	na
P_{vO_2} (mmHg)	74.3 $\pm$ 6.3 (10)	NS	-23.6 $\pm$ 4.3 (10)	-40.5 $\pm$ 7.8 (7)
C_{aO_2} ($\text{ml} \cdot \text{dl}^{-1}$)	32.3 $\pm$ 3.2 (9)	-1.2 $\pm$ 0.5 (7)	-4.5 $\pm$ 1.0 (9)	-8.7 $\pm$ 0.8 (6)
C_{vO_2} ($\text{ml} \cdot \text{dl}^{-1}$)	13.6 $\pm$ 1.2 (10)	-0.9 $\pm$ 0.4 (8)	-1.7 $\pm$ 0.7 (10)	-2.4 $\pm$ 0.5 (7)
$C_{\text{aO}_2} - C_{\text{vO}_2}$ ($\text{ml} \cdot \text{dl}^{-1}$)	9.0 $\pm$ 0.8 (9)	NS	NS	-2.4 $\pm$ 0.4 (6)
P_{aCO_2} (mmHg)	4.9 $\pm$ 0.8 (9)	-1.1 $\pm$ 0.4 (7)	NS	NS
P_{vCO_2} (mmHg)	3.3 $\pm$ 0.4 (8)	-0.3 $\pm$ 0.1 (7)	NS	NS
pHa	3.8 $\pm$ 0.5 (8)	NS	NS	-0.8 $\pm$ 0.3 (7)
pHv	7.82 $\pm$ 0.03 (10)	+0.02 $\pm$ 0.01 (8)	+0.05 $\pm$ 0.01 (10)	-0.6 $\pm$ 0.2 (6)
pHa - pHv	7.83 $\pm$ 0.02 (9)	NS	NS	+0.06 $\pm$ 0.01 (7)
O_2 delivery ($\text{ml} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	-0.01 $\pm$ 0.02 (9)	NS	+0.04 $\pm$ 0.01 (8)	NS
$\dot{V}_{\text{O}_2}$ -body ($\text{ml} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	14.5 $\pm$ 1.5 (8)	NS	NS	+0.06 $\pm$ 0.01 (6)
$\dot{V}_{\text{O}_2}$ -total ($\text{ml} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	4.7 $\pm$ 0.4 (7)	-1.5 $\pm$ 0.4 (6)	NS	-6.3 $\pm$ 1.7 (7)
$\dot{V}_{\text{O}_2}$ -gill ($\text{ml} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	10.5 $\pm$ 0.5 (10)	+1.1 $\pm$ 0.5 (8)	NS	-1.3 $\pm$ 0.2 (6)
$\dot{V}_{\text{a}}$ ($\text{l} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	5.9 $\pm$ 0.8 (7)	+2.5 $\pm$ 0.7 (6)	NS	na
$\dot{Q}$ ($\text{ml} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	3.9 $\pm$ 0.1 (10)	+1.1 $\pm$ 0.8 (8)	+3.0 $\pm$ 0.1 (10)	na
$\dot{V}_{\text{a}}/\dot{Q}$	115.4 $\pm$ 17.4 (8)	NS	NS	+5.1 $\pm$ 0.3 (8)
$\dot{V}_{\text{a}}/\dot{Q}$ conductance	43.4 $\pm$ 8.8 (8)	+11.5 $\pm$ 2.6 (7)	+39.2 $\pm$ 6.7 (8)	-40.9 $\pm$ 17.4 (6)
ΔP_{g} (mmHg)	0.73 $\pm$ 0.10 (8)	+0.18 $\pm$ 0.08 (7)	+0.26 $\pm$ 0.10 (8)	+86.8 $\pm$ 7.8 (6)
TO_2 ($\text{ml} \cdot \text{min}^{-1} \cdot \text{mmHg}^{-1} \cdot \text{kg}^{-1}$)	62.3 $\pm$ 4.4 (9)	-9.3 $\pm$ 2.2 (7)	-27.6 $\pm$ 3.4 (9)	+0.58 $\pm$ 0.08 (6)
DO_2 ($\text{ml} \cdot \text{min}^{-1} \cdot \text{mmHg}^{-1} \cdot \text{kg}^{-1}$)	0.17 $\pm$ 0.02 (7)	+0.04 $\pm$ 0.01 (7)	+0.22 $\pm$ 0.06 (9)	na
U (%)	0.18 $\pm$ 0.02 (9)	+0.05 $\pm$ 0.01 (7)	+0.23 $\pm$ 0.07 (9)	na
E_{w} (%)	50.8 $\pm$ 2.3 (10)	-7.5 $\pm$ 1.8 (8)	-18.0 $\pm$ 4.0 (10)	na
E_{b} (%)	62.6 $\pm$ 2.7 (7)	-7.4 $\pm$ 2.7 (7)	-15.3 $\pm$ 5.3 (9)	na
HR ($\text{beats} \cdot \text{min}^{-1}$)	89.3 $\pm$ 0.4 (7)	NS	-23.7 $\pm$ 7.8 (9)	-17.3 $\pm$ 7.0 (6)
SV ($\text{ml} \cdot \text{beat}^{-1} \cdot \text{kg}^{-1}$)	96.7 $\pm$ 5.8 (10)	NS	NS	-26.8 $\pm$ 4.3 (7)
BP_{va} (mmHg)	1.3 $\pm$ 0.2 (8)	NS	NS	NS
BP_{da} (mmHg)	89.7 $\pm$ 8.1 (10)	NS	NS	NS
R_{branch} ($\text{mmHg} \cdot \text{ml}^{-1} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	32.6 $\pm$ 2.4 (10)	NS	NS	NS
R_{system} ($\text{mmHg} \cdot \text{ml}^{-1} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	0.71 $\pm$ 0.06 (8)	NS	NS	NS
R_{total} ($\text{mmHg} \cdot \text{ml}^{-1} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	0.33 $\pm$ 0.02 (8)	NS	NS	+0.25 $\pm$ 0.11 (6)
Cardiac power output ($\text{mW} \cdot \text{kg}^{-1}$)	1.05 $\pm$ 0.06 (7)	NS	NS	+0.12 $\pm$ 0.04 (6)
Hct (%)	27.2 $\pm$ 4.3 (8)	NS	NS	+0.37 $\pm$ 0.13 (6)
	26.7 $\pm$ 1.2 (10)	NS	NS	-11.7 $\pm$ 4.6 (6)

Number of fish is in parentheses; NS = not significantly different from normoxia values; na = data not available

cases a P -value lower than 0.05 was taken as the fiducial limit of significance. The grand means for the normoxic measurements were calculated by averaging data collected during the control period from all three trials for each individual to arrive at a mean value for each fish. These values were, in turn, averaged to determine the grand mean for the species. All values in the text, tables, and figures are expressed as mean $\pm$ standard error of the mean (SEM).

Results

Normoxia

There were no significant differences in mean control values measured immediately before each level of hypoxia. This indicates that both tuna species remained physiologically stable throughout the course of an experiment, or that randomizing the sequence of presentation of the three levels of hypoxia removed any effects of physiological changes occurring over time. Most of the 35 measured or calculated variables (Tables 1, 2) were

similar in skipjack and yellowfin tunas, with the exception of $\dot{V}O_{2\text{-total}}$, $\dot{V}O_{2\text{-gill}}$, $\dot{V}_g$, TO_2 , DO_2 , HR, and Hct, which were significantly higher in skipjack tuna, and E_b , which was significantly lower.

Hypoxia: yellowfin tuna

During the 50 mmHg trial, P_eO_2 sometimes equaled or exceeded P_iO_2 . Therefore, we assume that exhaled water samples became contaminated by surrounding water when mouth gape and opercular flair increased by a large degree. As a result, no P_eO_2 s or associated calculations ($\dot{V}O_{2\text{-total}}$, $\dot{V}O_{2\text{-gill}}$, ΔPg , TO_2 , DO_2 , U , or E_w) are reported for this level of hypoxia.

Exposure of yellowfin tuna to hypoxia eventually resulted in significant changes in all measured and calculated variables except pHv, SV, BP_{vis} , BP_{da} , and Hct (Table 1). When P_iO_2 was reduced to only 130 mmHg, P_aO_2 , P_vO_2 , and C_aO_2 were already significantly reduced,

Table 2. Mean values ($\pm$ SEM) of cardiorespiratory variables measured in normoxia and significant changes occurring during hypoxia in skipjack tuna (*Katsuwonus pelamis*)

Variable	Control	Hypoxia		
		($P_iO_2 \approx 130$ mmHg)	($P_iO_2 \approx 90$ mmHg)	($P_iO_2 \approx 50$ mmHg)
P_iO_2 (mmHg)	152.5 $\pm$ 1.2 (9)	-22.3 $\pm$ 3.0 (8)	-66.9 $\pm$ 2.7 (6)	-101.3 $\pm$ 2.4 (6)
P_eO_2 (mmHg)	74.7 $\pm$ 3.1 (9)	NS	-23.5 $\pm$ 6.1 (7)	na
P_aO_2 (mmHg)	69.7 $\pm$ 7.1 (9)	-7.1 $\pm$ 2.3 (6)	-26.7 $\pm$ 4.6 (8)	-51.3 $\pm$ 6.2 (6)
P_vO_2 (mmHg)	36.7 $\pm$ 3.0 (9)	-3.8 $\pm$ 0.6 (6)	-10.8 $\pm$ 1.9 (8)	-17.6 $\pm$ 3.8 (6)
C_aO_2 (ml $\cdot$ dl $^{-1}$)	15.1 $\pm$ 2.1 (9)	NS	-1.9 $\pm$ 0.8* (8)	-5.5 $\pm$ 1.7* (6)
C_vO_2 (ml $\cdot$ dl $^{-1}$)	10.0 $\pm$ 1.5 (9)	NS	-2.3 $\pm$ 0.5 (8)	-3.9 $\pm$ 0.7 (6)
$C_aO_2 - C_vO_2$ (ml $\cdot$ dl $^{-1}$)	5.1 $\pm$ 0.9 (9)	NS	NS	NS
P_aCO_2 (mmHg)	3.0 $\pm$ 0.4 (9)	NS	NS	-0.8 $\pm$ 0.2
P_vCO_2 (mmHg)	3.8 $\pm$ 0.5 (8)	NS	NS	-0.4 $\pm$ 0.2 (6)
$P_aCO_2 - P_vCO_2$ (mmHg)	7.86 $\pm$ 0.03 (9)	+ 0.03 $\pm$ 0.004 (6)	+ 0.06 $\pm$ 0.01 (8)	+ 0.12 $\pm$ 0.03 (6)
pHa	7.86 $\pm$ 0.04 (9)	NS	+ 0.03 $\pm$ 0.01 (8)	NS
pHv	-0.01 $\pm$ 0.01 (9)	NS	+ 0.03 $\pm$ 0.01 (8)	+ 0.11 $\pm$ 0.02 (6)
pHa - pHv	18.2 $\pm$ 3.4 (9)	NS	-5.8 $\pm$ 1.5 (8)	-11.3 $\pm$ 2.3 (6)
O_2 delivery (ml $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	5.8 $\pm$ 1.0 (9)	NS	NS	NS
$\dot{V}O_{2\text{-body}}$ (ml $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	18.2 $\pm$ 0.7# (9)	NS	NS	na
$\dot{V}O_{2\text{-total}}$ (ml $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	12.4 $\pm$ 0.8# (9)	NS	NS	na
$\dot{V}O_{2\text{-gill}}$ (ml $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	6.8 $\pm$ 0.1# (9)	+ 0.8 $\pm$ 0.1 (5)	+ 2.4 $\pm$ 0.1 (8)	+ 3.7 $\pm$ 0.1 (7)
$\dot{V}_g$ (l $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	132.3 $\pm$ 26.5 (9)	NS	-27.0 $\pm$ 12.7 (8)	-57.3 $\pm$ 16.4 (6)
$\dot{Q}$ (ml $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	71.8 $\pm$ 13.3 (9)	NS	+44.0 $\pm$ 12.3 (8)	+99.6 $\pm$ 20.5 (6)
$\dot{V}_g/\dot{Q}$	1.09 $\pm$ 0.16 (9)	NS	NS	+0.53 $\pm$ 0.17 (6)
$\dot{V}_g/\dot{Q}$ conductance	60.5 $\pm$ 4.8 (9)	NS	-29.4 $\pm$ 5.3 (8)	na
ΔPg (mmHg)	0.32 $\pm$ 0.03# (9)	NS	+0.32 $\pm$ 0.10 (8)	na
TO_2 (ml $\cdot$ min $^{-1}$ $\cdot$ mmHg $^{-1}$ $\cdot$ kg $^{-1}$)	0.35 $\pm$ 0.03# (9)	NS	+0.22 $\pm$ 0.07 (7)	na
DO_2 (ml $\cdot$ min $^{-1}$ $\cdot$ mmHg $^{-1}$ $\cdot$ kg $^{-1}$)	51.0 $\pm$ 2.0 (9)	-10.2 $\pm$ 3.1 (8)	NS	na
U (%)	67.4 $\pm$ 2.9 (9)	-12.3 $\pm$ 4.3 (6)	NS	na
E_w (%)	74.1 $\pm$ 1.5# (9)	NS	-9.3 $\pm$ 4.5	-26.7 $\pm$ 10.2 (6)
E_b (%)	125.9 $\pm$ 14.8# (9)	-14.1 $\pm$ 4.5 (6)	-31.5 $\pm$ 9.1 (8)	-48.0 $\pm$ 9.7 (6)
HR (beats $\cdot$ min $^{-1}$)	1.1 $\pm$ 0.1 (9)	NS	NS	-0.13 $\pm$ 0.06 (6)
SV (ml $\cdot$ beat $^{-1}$ $\cdot$ kg $^{-1}$)	87.3 $\pm$ 5.4 (8)	NS	NS	NS
BP_{vis} (mmHg)	40.2 $\pm$ 3.4 (9)	NS	-4.0 $\pm$ 1.4 (7)	NS
BP_{da} (mmHg)	0.43 $\pm$ 0.06 (8)	NS	+0.13 $\pm$ 0.06 (6)	+0.31 $\pm$ 0.08 (5)
R_{branch} (mmHg $\cdot$ ml $^{-1}$ $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	0.33 $\pm$ 0.07 (9)	NS	NS	NS
R_{system} (mmHg $\cdot$ ml $^{-1}$ $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	0.74 $\pm$ 0.16 (8)	NS	NS	+0.46 $\pm$ 0.12 (5)
R_{total} (mmHg $\cdot$ ml $^{-1}$ $\cdot$ min $^{-1}$ $\cdot$ kg $^{-1}$)	29.2 $\pm$ 0.9 (7)	NS	-6.2 $\pm$ 2.8 (7)	-11.4 $\pm$ 3.7 (5)
Cardiac power output (mW $\cdot$ kg $^{-1}$)	33.9 $\pm$ 1.4# (8)	NS	NS	NS
Hct (%)				

Denotes significant difference between skipjack and yellowfin tunas during normoxia
 Number of fish is in parentheses; NS = not significantly different from normoxia values; na = data not available

and all continued to decrease as hypoxia became more severe. C_vO_2 was maintained at control values until P_iO_2 was reduced to 50 mmHg, by which time it had fallen significantly. $C_aO_2 - C_vO_2$ difference was reduced at 130 mmHg, but not at 90 and 50 mmHg. A significant decrease in P_aCO_2 resulted in a significant increase in pHa at all levels of hypoxia. However, P_aCO_2 did not decrease until yellowfin tuna were exposed to the most intense level of hypoxia. As a result, pH_v was maintained at control levels throughout, producing a significant $pHa - pH_v$ difference at 90 and 50 mmHg. The lack of bradycardia at 130 and 90 mmHg allowed $\dot{O}_2$ delivery to be maintained at normoxic levels during moderate hypoxia, despite the slight fall in C_aO_2 . At 50 mmHg, a significant bradycardia occurred and $\dot{Q}$ fell because SV did not increase; consequently, O_2 delivery fell. Blood pressure remained unchanged during a 36% fall in $\dot{Q}$ at 50 mmHg. This indicates that a general vasoconstriction had occurred, as shown by significant increases in R_{branch} , R_{system} , and R_{total} . The reduced $\dot{Q}$ at this level of hypoxia also resulted in a significant reduction in cardiac power output.

The $C_aO_2 - C_vO_2$ difference, which was reduced at 130 mmHg because of the fall in C_aO_2 , regained normoxic values at 90 and 50 mmHg because of a decline in C_vO_2 . $\dot{V}O_{2-body}$ was significantly lower at 130 mmHg as a consequence of the smaller $C_aO_2 - C_vO_2$ difference; it returned to normoxic levels when P_iO_2 was reduced to 90 mmHg, as the $C_aO_2 - C_vO_2$ difference also returned to control values. $\dot{V}O_{2-body}$ was significantly reduced at 50 mmHg because $\dot{Q}$ fell. As a result of a significant increase in $\dot{V}O_{2-total}$ concomitant with the decrease in $\dot{V}O_{2-body}$ at 130 mmHg, $\dot{V}O_{2-gill}$ was elevated at 130 mmHg, but returned to normoxic levels at 90 mmHg.

Gas exchange variables were also sensitive to changes in P_iO_2 . As $\dot{V}_g$ increased during hypoxia, the $\dot{V}_g/\dot{Q}$ ratio rose significantly through all levels of hypoxia to a high of 125 at 50 mmHg. Although a reduction in U occurred as a consequence of the increased $\dot{V}_g$, it was not enough to prevent the $\dot{V}_g/\dot{Q}$ conductance ratio from increasing as hypoxia became more severe. Despite a significant increase in TO_2 and DO_2 at 130 and 90 mmHg, E_w fell at 130 and 90 mmHg. E_b remained at normoxic levels at 130 mmHg, but was significantly reduced at both 90 and 50 mmHg.

Hypoxia: skipjack tuna

As in yellowfin tuna, exhaled water samples apparently became contaminated by surrounding water during the 50 mmHg hypoxia trial. Therefore, no P_aO_2 s or associated calculations ($\dot{V}O_{2-total}$, $\dot{V}O_{2-gill}$, ΔPg , TO_2 , DO_2 , U , or E_w) are reported for this level of hypoxia.

Changes believed to be indicative of failure in the oxygen extraction and delivery systems occurred at moderate levels of hypoxia (Table 2). Significant bradycardia occurred at 130 mmHg and became more severe as hypoxia deepened. This resulted in a significant reduction

in $\dot{Q}$ at 90 mmHg which, along with a decrease in C_aO_2 , caused O_2 delivery to begin to decline. Other aspects of the skipjack tuna's inability to tolerate hypoxia included a relatively slow increase in TO_2 and DO_2 , neither of which changed until P_iO_2 was reduced to 90 mmHg. Interestingly, E_w was significantly reduced at 130 mmHg but not at 90 mmHg, while E_b was unchanged at 130 mmHg, but significantly reduced at 90 mmHg and further reduced at 50 mmHg. The increase in $\dot{V}_g/\dot{Q}$ ratio observed at every level of hypoxia was accompanied by an increase of $\dot{V}_g/\dot{Q}$ conductance only when P_iO_2 had fallen to 50 mmHg.

Because the decrement in C_aO_2 was accompanied by a fall in C_vO_2 , the arterial-venous oxygen content difference never varied significantly from control measurements. P_aCO_2 was reduced at all levels of hypoxia. Therefore, pHa was significantly increased, and the $pHa - pH_v$ difference became significant at 90 and 50 mmHg.

BP_{da} was essentially maintained despite significant reductions in $\dot{Q}$ at 90 and 50 mmHg. However, statistically significant increases in R_{branch} and R_{total} occurred only at a P_iO_2 of 50 mmHg. Cardiac power output was reduced at 90 mmHg because of the lowered $\dot{Q}$ and was reduced by approximately 60% at 50 mmHg because of the steep reduction in $\dot{Q}$.

Discussion

Cardiovascular function during normoxia. The P_aO_2 values of skipjack and yellowfin tunas (69.7 and 74.3 mmHg, respectively) in this study are similar to those found in paralyzed force-ventilated albacore (*Thunnus alalunga*) [62 mmHg, White et al. (1988)] but are lower than those of lightly anesthetized, force-ventilated skipjack tuna [90 mmHg, Stevens (1972)]. More important, our values nearly match those found in free-swimming kawakawa (*Euthynnus affinis*) [63 mmHg, Jones et al. (1986)], indicating that the P_aO_2 values for the fish in this study were not abnormal nor an artifact caused by surgical and other manipulations. P_aO_2 values in tunas are, surprisingly, much lower than those in conscious but sedentary rainbow trout [130 mmHg, Holeyton and Randall (1967b), Kiceniuk and Jones (1977)]. The reasons for these differences are unknown. Note however, that during normoxia arterial blood is more than 80% saturated in skipjack tuna and more than 90% saturated in yellowfin tuna (Fig. 1).

P_aO_2 values are similar to those of force-ventilated skipjack tuna [32 mmHg, Stevens (1972)] and rainbow trout [30 mmHg, Holeyton and Randall (1967a) and Kiceniuk and Jones (1977)] but are higher than those of force-ventilated albacore [12 mmHg, White et al. (1988)] and free-swimming kawakawa [13 mmHg, Jones et al. (1986)]. This is presumably due to oxygen demands being higher in the albacore which had been recently boated and were recovering from the stress of capture, and in the swimming kawakawa which had towed a number of catheters.

Arterial blood oxygen content in most other teleosts ranges from 4 to 10 ml · dl⁻¹, and those of tuna were thought to be much higher (Randall 1970). An unusually high C_aO₂ of 21.7 ml · dl⁻¹ was reported by White et al. (1988) in stressed, freshly boated albacore that had Hcts of over 50%. We found the Hct in skipjack and yellowfin tunas to be substantially lower (27–33%) and similar to that (35%) reported by Jones et al. (1986) in free-swimming kawakawa. As a result, the C_aO₂s reported here are also lower than that found by White et al. (1988). Because we often saw Hcts of over 50% in yellowfin and skipjack tunas that had been netted and had blood sampled by cardiac puncture, we believe the reports of unusually high Hct and oxygen-carrying capacity of tuna blood to be a result of either the release of red cells into the circulation from the spleen or hemoconcentration. Both occur during capture or exercise in other teleosts (Yamamoto and Itazawa 1989).

The spinally blocked (i.e., non-swimming) tunas in this study maintained a significantly higher venous oxygen reserve (C_vO₂ was approximately 40–60% of C_aO₂) than observed in other teleosts. For example, in rainbow trout C_vO₂ is only 14% of C_aO₂ (Kiceniuk and Jones 1977). A high C_vO₂ level also been observed in paralyzed, force-ventilated albacore (White et al. 1988). However, the lower P_vO₂ seen in swimming kawakawa (Jones et al. 1986) implies that the high venous reserve seen in non-swimming tunas may be due to low oxygen consumption of the swimming muscles.

P_aCO₂ and P_vCO₂ recorded previously in tunas [4.1–5.5 and 5.5 mmHg, respectively; (Jones et al. 1986; White et al. 1988)] are only slightly higher than those reported here (3.0–3.3 and 3.8 mmHg, respectively). The kawakawa from which Jones et al. (1986) collected blood were free swimming, yet the investigators thought the fish were under ventilated and therefore had significantly elevated blood CO₂ levels. In light of our data, this apparently is not the case. White et al. (1988) found elevated P_vCO₂ (9.0 mmHg) and low pH_v (7.55) in albacore, presumably because these fish were still recovering from the stress of capture. Finally, studies by Perry et al. (1985) and Brill et al. (1991) have shown that blood from skipjack and yellowfin tunas has a very high non-bicarbonate buffering capacity; therefore, the lack of an arterial to venous pH difference in our study is not surprising.

$\dot{Q}$ measured in this study (115–132 ml · min⁻¹ · kg⁻¹) were significantly above those recorded in albacore [29.4–36.1 ml · min⁻¹ · kg⁻¹; Lai et al. (1987), White et al. (1988)], although part of this difference may be explained by the albacore being much larger (7.4–11.2 kg body weight) than the fish studied here. Surprisingly, our measures of $\dot{Q}$ are close to that for skipjack tuna calculated using the Fick equation [80–100 ml · min⁻¹ · kg⁻¹; (Stevens 1972; Brill et al. 1978)] despite the fact that the large gill $\dot{V}$ O₂ of tunas (discussed below) would cause the Fick method to over estimate $\dot{Q}$ (Metcalf and Butler 1982). This apparent paradox remains to be resolved. Although affected by differences in body size and measurement temperature,

the $\dot{Q}$ of skipjack and yellowfin tuna are approximately 3–10 times those recorded in other teleosts such as rainbow trout [17.6 ml · min⁻¹ · kg⁻¹, Kiceniuk and Jones (1977)], cod [*Gadus morhua*, 19.2 ml · min⁻¹ · kg⁻¹, Fritzsche and Nilsson (1989)] or eel [*Anguilla anguilla*, 11.5 ml · min⁻¹ · kg⁻¹, Peyraud-Waitzenegger and Soulier (1989)].

HRs measured in this study were similar to those recorded previously (Bushnell et al. 1990). In spite of the higher HR of skipjack tuna, SV values were similar (1.1–1.3 ml · beat⁻¹ · kg⁻¹) in both species and comparable to that calculated for skipjack tuna from data presented in Stevens (1972). SV in skipjack and yellowfin tunas, however, are substantially higher than those recorded by White et al. (1988) and Lai et al. (1987) in 9- to 10-kg albacore (0.33–0.36 ml · beat⁻¹ · kg⁻¹). Both HR and SV in skipjack and yellowfin tuna are also significantly higher than those of other teleosts such as rainbow trout [37.8 beats · min⁻¹ and 0.46 ml · beat⁻¹ · kg⁻¹ (Kiceniuk and Jones 1977)], cod [41.4 beats · min⁻¹ and 0.51 ml · beat⁻¹ · kg⁻¹ (Fritzsche and Nilsson 1989)] or eel [37.1 beats · min⁻¹ and 0.29 ml · beat⁻¹ · kg⁻¹ (Peyraud-Waitzenegger and Soulier 1989)].

Although high when compared with those in salmonids [30–70 mmHg (Holeton and Randall 1967a; Randall 1970)], the BP_{va} values in yellowfin and skipjack tunas in our study (87–90 mmHg) are in good agreement with those of Lai et al. (1987) for albacore. Interestingly, White et al. (1988) reported similar mean BP_{va} values in albacore, but mean BP_{da} values that were only 1–5 mmHg lower. In this study, blood pressure drop across the gills was 56 and 47 mmHg in yellowfin and skipjack tunas, respectively. Muir and Brown (1971) speculated that the oblique blood channels through the secondary lamellae of tuna are an adaptation to reduce the blood pressure drop across the gills. In support of this argument, they used morphometric and physiological data to calculate the BP_{va} – BP_{da} differences when blood was flowing along the transverse length of the secondary lamellae or the shorter oblique channels. The drop in blood pressure predicted for the long transverse channels (68 mmHg) is close to that recorded here and by Lai et al. (1987), while the 3.9 mmHg reduction, calculated to result from blood flowing through the shorter oblique channels, is close to that observed by White et al. (1988). Typically, the branchial vasculature resistance represents 20–40% of the total vascular resistance in fishes. The R_{branch} in our study was 60% and 68% of R_{total} in skipjack and yellowfin tunas, respectively, but was only 26% and 4% of R_{total} using data for albacore presented in Lai et al. (1987) and White et al. (1988), respectively. Whether tunas can rearrange blood flow within the gill to bring about a significant modification of vascular resistance, as these data imply, remains to be determined.

Because of the high $\dot{Q}$ and BP_{va}, the cardiac power output of yellowfin and skipjack tunas exceeds that of other active species (e.g., rainbow trout) by approximately an order of magnitude (Brill and Bushnell 1991b).

Cardiorespiratory function during normoxia. Despite differences of an order of magnitude or more in $\dot{V}_g$ (and $\dot{V}O_2$) of starry flounder [*Platichthys stellatus*; $\dot{V}_g = 0.111 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ (Wood et al. 1979)], tench [*Tinca tinca*; $\dot{V}_g = 0.121 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ (Eddy 1974)], rainbow trout [$\dot{V}_g = 0.171 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$; Cameron and Davies (1970)], and eel [$\dot{V}_g = 0.084 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ (Peyraud-Waitzenegger and Soulier 1989)], skipjack tuna ($6.81 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) and yellowfin tuna ($3.91 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) (Stevens 1972; this study), all utilize approximately 50% of the oxygen in the water passing over the gills.

The $\dot{V}_g/\dot{Q}$ ratio in teleosts other than tunas ranges from 1.04 and 2.94 in the rainbow trout and starry flounder, respectively (Cameron and Davis 1970; Wood et al. 1979) to 7.34 and 8.25 in the eel and tench, respectively (Eddy 1974; Peyraud-Waitzenegger and Soulier 1989). The $\dot{V}_g/\dot{Q}$ ratio of skipjack and yellowfin tunas (Tables 1, 2) is much higher because of their higher $\dot{V}_g$. However, $\dot{V}_g/\dot{Q}$ conductance ratio, which takes into account differences in blood oxygen-carrying capacity, indicates that the ventilation/perfusion systems are well matched in skipjack tuna (1.09), while yellowfin tuna are slightly over-perfused (0.73). Previous studies in teleosts and elasmobranchs have found $\dot{V}_g/\dot{Q}$ conductance to vary from 0.42 in the larger spotted dogfish, *Scyliorhinus stellaris*, and 1.8 in the dogfish, *S. canicula* (Short et al. 1979), to 1.2 in rainbow trout (Randall et al. 1967). Based on theoretical grounds, a slight over-ventilation is considered advantageous for maintaining a high P_{aO_2} (Scheid and Piiper 1976).

The TO_2 s measured in our study (0.32 and $0.17 \text{ ml} \cdot \text{min}^{-1} \cdot \text{mmHg}^{-1} \cdot \text{kg}^{-1}$ in skipjack and yellowfin tunas, respectively) are the highest recorded in any species to date and are similar to those made by Stevens (1972) for force-ventilated skipjack tuna. In contrast, the TO_2 s of eel, tench, starry flounder, dogfish, and rainbow trout are only 0.0045 (Peyraud-Waitzenegger and Soulier 1989), 0.0061 (Eddy 1974), 0.0069 (Wood et al. 1979), 0.013 (Short et al. 1979), and 0.016 (Cameron and Davis 1970) $\text{ml} \cdot \text{min}^{-1} \cdot \text{mmHg}^{-1} \cdot \text{kg}^{-1}$, respectively. The diffusion capacity (DO_2), a related measure of oxygen transfer that incorporates the properties of hemoglobin (Eqs. 11, 12), was not significantly different from TO_2 in skipjack and yellowfin tunas, as was also found by Short et al. (1979) in the dogfish. Unfortunately, there are few reported measures of DO_2 in other species.

TO_2 and DO_2 depend primarily on the gill surface area available for exchange, and diffusion distance between blood and water (Randall et al. 1967). When corrected for size, a 200-g skipjack tuna has a gill surface area of 2051 mm^2 compared to a similarly sized rainbow trout which has a gill surface area of only 206 mm^2 . In general, tunas have gill surface areas 5–10 times larger than other active teleosts (Hughes 1984a, b). In addition, the mean total water-blood distance in the secondary lamellae of tuna gills is very small, being only 0.60 and 0.53 μm in skipjack and yellowfin tunas, respectively, but 6.37 μm in rainbow trout (Hughes 1984a).

The fact that the P_{aO_2} did not equal P_{iO_2} suggests that the gills are not acting as perfect counter-current gas

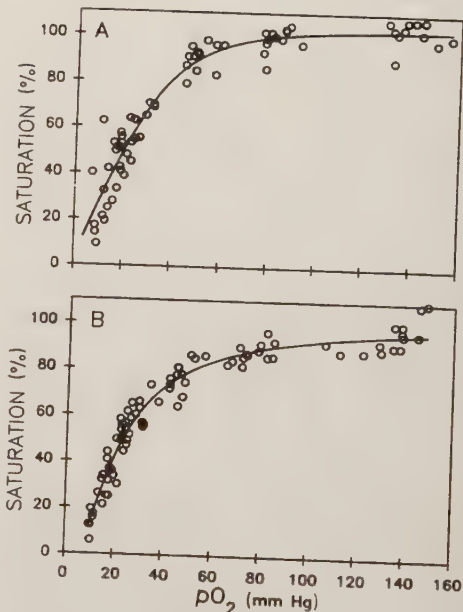


Fig. 1A, B. Blood oxygen dissociation curves for yellowfin tuna (A) and skipjack tuna (B). Data are from blood equilibrated at 20 and 30 °C with 0.5% CO_2 (i.e., arterial PCO_2) and various oxygen tensions. The P_{50} s for yellowfin and skipjack tuna were 20.5 and 22.5 mmHg, respectively. The plasma pHs at P_{50} were 7.876 and 7.925, respectively. Data were taken from the study on the effects of temperature on tuna blood oxygen binding characteristics by Brill and Bushnell (1991)

exchangers for oxygen. Indications of where departures from the ideal occur are provided by measurements of E_w and E_g . E_w values in both skipjack and yellowfin tunas (67% and 63%, respectively) were lower than previously estimated for skipjack tuna [90% (Stevens 1972)], but higher than those for rainbow trout [30–58% (Randall et al. 1967; Cameron and Davis 1970)], and dogfish [29% (Short et al. 1979)], and roughly equal to that of a starry flounder [75% (Wood and Shelton 1979)]. The average E_w of 65% in the tunas means that at least 65% of the water flowing past the gills was effectively “in contact” with blood in the gills, or conversely, only 35% of the water was “shunted” into pathways that did not participate in oxygen exchange (Piiper and Scheid 1984). With such a large $\dot{V}_g$, the fact that E_w is not lower is an indicator of the efficiency of tuna gills as a gas exchanger.

E_g s in starry flounder, tench, rainbow trout, and dogfish are 57, 81, 90, and 91%, respectively (Randall 1967; Randall et al. 1967; Short et al. 1979; Wood et al. 1979); in this study E_g s in skipjack and yellowfin tunas were 74 and 89%, respectively. The fact that E_g was relatively low in skipjack tuna indicates that measured C_{O_2} s were substantially less than they would have been if P_{aO_2} equaled P_{iO_2} and blood leaving the gills was nearly saturated (see Eq. 10). In most fishes, blood leaving the gills is over 90% saturated, and the hemoglobin is functioning on the top (i.e., relatively flat) portion of the

oxygen dissociation curve (Cameron 1971; Eddy 1973). Therefore, large P_{iO_2} - P_{oO_2} differences have little effect on C_{aO_2} . However, based on the blood oxygen dissociation curves (Fig. 1), blood leaving the gills in skipjack tuna (but not yellowfin tuna) is operating near the shoulder or steep portion of the dissociation curve, where C_{aO_2} falls rapidly with P_{O_2} . This may be due to the high oxygen demand of the gill tissue itself (discussed in the following section). In other words, the oxygen needed to meet the energy demands of the gill tissue in skipjack tuna may be taken from the blood as well as the water. However, it more likely that the differences in E_b between skipjack and yellowfin tunas is due to the differences in shapes of the blood oxygen dissociation curves at their upper ends. Yet to be determined is whether this situation changes during the increased periods of oxygen demand during high speed swimming and oxygen debt repayment.

Metabolic costs of large gill surface areas. The gills are the main sites of passive water and ion movements and are also the main organ of osmoregulation (Evans 1979). Therefore, fish (such as tunas) with large gill surface areas are likely to have high osmoregulatory costs (Stevens 1972; Brill 1987), much of which will occur at the gills. The cost of osmoregulation has been estimated to account for 27–50% of the standard metabolic rate (Rao 1968; Nordlie and Leffler 1975), and Daxboeck et al. (1982) estimated that the metabolism of the gills alone accounts for 27% (range 19–75%) of the standard metabolic rate of rainbow trout. In our study, $\dot{V}O_{2\text{-gill}}$ accounted for 68% and 54% of $\dot{V}O_{2\text{-total}}$ in skipjack and yellowfin tunas, respectively. When expressed as oxygen demand per unit gill surface area of a 1-kg fish (Hughes 1984a), the $\dot{V}O_{2\text{-gill}}$ of skipjack and yellowfin tunas ($6.70 \cdot 10^{-6}$ and $4.43 \cdot 10^{-6} \text{ ml} \cdot \text{min}^{-1} \cdot \text{mm}^{-2}$, respectively) are substantially higher than that of (fresh-water) rainbow trout [$0.77 \cdot 10^{-6} \text{ ml} \cdot \text{min}^{-1} \cdot \text{mm}^{-2}$ (Daxboeck et al. 1982)] but equivalent to that of (sea water) Atlantic cod, *Gadus morhua* [$8.59 \cdot 10^{-6} \text{ ml} \cdot \text{min}^{-1} \cdot \text{mm}^{-2}$; (Johansen and Pettersson 1981)].

Cardiovascular and cardiorespiratory function during hypoxia. Studies using spinally blocked (force-ventilated) and free-swimming skipjack and yellowfin tunas showed that both species increased gape and $\dot{V}_g$ in response to hypoxia (Bushnell et al. 1990; Bushnell and Brill 1991). Although $\dot{V}_g$ could not be quantified in this study, an increase in mouth gape occurred, and it is assumed that $\dot{V}_g$ increased during hypoxia in a manner similar to that recorded previously.

Stevens (1972) observed a significant negative correlation between $\dot{V}_g$ and U in force-ventilated skipjack tuna during normoxia, as did Bushnell and Brill (1991) in free-swimming yellowfin tuna during hypoxia. Therefore, increased $\dot{V}_g$ probably accounts for some of the observed 14–35% decrease in U observed in this study during hypoxia. During an approximate doubling of $\dot{V}_g$ in response to hypoxia, U decreased 17–35% in flounder, rainbow trout, and European eel (Kerstens et al.

1979; Smith and Jones 1982; Steffensen et al. 1982; Le Moigne et al. 1986). A decrease in U , concomitant with a increase in $\dot{V}_g$ during hypoxia is not a universal response in fishes, however. In studies of spiny dogfish (Short et al. 1979), catfish *Ictalurus punctatus* (Burggren and Cameron 1980), plaice *Pleuronectes platessa* (Steffensen et al. 1982), and European eel (Peyraud-Waitzenegger and Soulier 1989), no changes in U were found during hypoxia despite increases in $\dot{V}_g$.

Significant bradycardia occurred at P_{iO_2} values of 90 and 50 mmHg in skipjack tuna, but not until P_{iO_2} reached 50 mmHg in yellowfin tuna. These data agree with those previously obtained for spinally blocked and swimming skipjack tuna, although the HR response of yellowfin tuna in the present study appeared less sensitive to hypoxia than that reported in Bushnell et al. (1990) and Bushnell and Brill (1991).

$\dot{Q}$ decreased by 19% and 42% in skipjack tuna at P_{iO_2} values of 90 and 50 mmHg, respectively, and by 36% in yellowfin tuna at a P_{iO_2} of 50 mmHg. The reductions in $\dot{Q}$ at a P_{iO_2} of 50 mmHg are similar to those observed in lingcod (*Ophiodon elongatus*) and European eel (31% and 37% reduction in $\dot{Q}$, respectively) at similar levels of hypoxia (Farrell 1982; Peyraud-Waitzenegger and Soulier 1989). However, Atlantic cod and rainbow trout maintain $\dot{Q}$ down to a P_{iO_2} of 30–40 mmHg (Wood and Shelton 1980; Fritsche and Nilsson 1989) and dogfish sharks down to a P_{iO_2} of 77 mmHg (Short et al. 1979), in spite of significant bradycardia, by increasing in SV. In contrast, skipjack and yellowfin tunas showed no increases in SV.

The increase in SV during hypoxia-induced bradycardia has been attributed to a Starling response and an increase in circulating catecholamines compensating for the depressant effect of hypoxia on myocardial contractility (Short et al. 1977; Farrell 1985). In eels studied by Peyraud-Waitzenegger and Soulier (1989), there was no increase in circulating catecholamines during hypoxia and no increase in SV. The same situation could be occurring in tunas during hypoxia; however, another explanation is more likely: recent studies by Farrell et al. (1990) on the isolated, perfused hearts of skipjack and yellowfin tunas indicated that tuna hearts normally function on the upper (i.e., flat) portion of their Starling curves, and therefore the increased filling time during bradycardia can not result in compensatory increases in SV.

In both skipjack and yellowfin tunas, blood pressures remained essentially unchanged at all levels of hypoxia because of a general vasoconstriction (i.e., increases in R_{total} , R_{branch} , and R_{system}). In yellowfin tuna, the percentage drop in $\dot{Q}$ was similar to the increases in R , suggesting that increases in R may have resulted from passive "collapse" of elastic blood vessels (Farrell 1984). However, reflex vasoactivity may also have occurred in which the reflex arc involved afferent information from baroreceptors and efferent information to branchial and systemic receptors as has been observed in other teleosts (Farrell 1984; Fritsche and Nilsson 1990). Direct hypoxic vasoconstriction of the gills may also occur in tunas as in other teleosts (Pettersson and Johansen 1982). Blood

pressure responses to hypoxia appear to be species specific, however, because increases (Holeton and Randall 1967b; Fritzsche and Nilsson 1989, 1990), decreases (Farrell 1982; Peyraud-Waitzenegger Soulier 1989), and no change (Fritzsche 1990) have been observed.

The dramatic reduction in cardiac power output in skipjack tuna at a P_{iO_2} of 50 mmHg may be indicative of general myocardial failure. Nothing is known about the hypoxia tolerance of tuna myocardium, although our data suggest that it is relatively hypoxia intolerant. The high myoglobin levels observed in tuna hearts (Giovane et al. 1980) may, therefore, not function to maintain contractility in the face of low extracellular oxygen as has been suggested for other teleosts (Dreidzic 1983, 1988); rather, high myoglobin levels may serve to ensure adequate rates of oxygen delivery to the mitochondria, as they apparently do in tuna red muscle (Stevens 1972).

TO_2 in skipjack tuna remained unchanged at a P_{iO_2} of 130 mmHg, but doubled when P_{iO_2} was reduced to 90 mmHg. In yellowfin tuna, TO_2 increased by 23% at 130 mmHg and 122% at a P_{iO_2} of 90 mmHg. In spiny dogfish, TO_2 showed no change during hypoxia, but in European eel it increased 66% at a P_{iO_2} of 40 mmHg. DO_2 increased in both tuna species during hypoxia. The increase, which occurred at a higher P_{iO_2} in yellowfin tuna (130 mmHg) than in skipjack tuna (90 mmHg), was a result of a decrease in the mean water to blood PO_2 gradient (ΔP_g), which also appears to account for the entire change in TO_2 . The fact that an already high normoxic TO_2 or DO_2 was increased further is indicative of the excellent gas-exchange capabilities of the gills of tunas.

Increases in TO_2 and DO_2 imply an increase in the effective gill surface area, or a reduction in the diffusion distance between blood and water, or both. The effective area of the gills can be increased by lamellar recruitment, redistribution of blood flow, or distention of secondary lamellae due to increase in systolic or pulse pressures (Randall et al. 1967; Jones and Randall 1978; Booth 1979; Farrell 1980; Davie et al. 1982; Pettersson and Johansen 1982). At present it is not known whether lamellar recruitment can occur in tunas. An increase in blood pressure thought to promote lamellar recruitment (Booth 1979) was not seen in our study, however. Hypoxic bradycardia per se may also be partially responsible for the observed increases in TO_2 and DO_2 . Abolition of the hypoxic bradycardia with atropine abated the increases observed in dogfish at a P_{iO_2} of 50 mmHg (Taylor and Barrett 1985).

Another important determinant of gas transfer efficiency is the coupling of the respiratory and circulatory systems, as reflected in the $\dot{V}_g/\dot{Q}$ and the $\dot{V}_g/\dot{Q}$ conductance ratios. Both increased at all levels of hypoxia in yellowfin tuna, which actually become over-ventilated (i.e., $\dot{V}_g/\dot{Q}$ conductance ratio > 1). Skipjack tuna, in contrast, showed significant increase in $\dot{V}_g/\dot{Q}$ at P_{iO_2} levels of 90 and 50 mmHg, whereas $\dot{V}_g/\dot{Q}$ conductance ratio increased only at a P_{iO_2} of 50 mmHg. The doubling of the $\dot{V}_g/\dot{Q}$ observed at a P_{iO_2} of 50 mmHg is slightly less than the threefold increase recorded previously by Bushnell et al. (1990), but is much less than the 13-fold in-

crease recorded in rainbow trout under similar conditions (Holeton and Randall 1967a; Wood and Shelton 1980).

$\dot{V}_g/\dot{Q}$ conductance did not rise more rapidly during hypoxia because the increase in the ventilatory oxygen delivery was offset for a time by the increase in the oxygen solubility of the blood. As the P_{aO_2} fell during hypoxia, the blood began to function on the shoulder or steeper portion of the dissociation curve. As a consequence, large changes in oxygen content occurred in association with small changes in P_{aO_2} , and the solubility coefficient increased. The largest increase in $\dot{V}_g/\dot{Q}$ conductance occurred at a P_{iO_2} of 50 mmHg when the concomitant reduction in $\dot{Q}$ reached its maximum.

E_w decreased 17% and 12% at a P_{iO_2} of 130 mmHg in skipjack and yellowfin tunas, respectively. It declined 24% at a P_{iO_2} of 90 mmHg in yellowfin tuna, but was unchanged at this level of hypoxia in skipjack tuna. This occurred in spite of predicted $\dot{V}_g$ being significantly increased at both levels of hypoxia in both species. In comparison, E_w in trout (Randall et al. 1967), dogfish (Short et al. 1979), and European eel (Peyraud-Waitzenegger and Soulier 1989) remains unchanged during hypoxia. E_b decreased during hypoxia (at 90 and 50 mmHg) in both skipjack and yellowfin tunas. Hypoxia (P_{iO_2} 80 mmHg) has been shown to decrease E_b in dogfish, an effect which was attributed to fact that arterial blood was functioning below the shoulder of the oxygen dissociation curve (Short et al. 1979). Based on P_{aO_2} s recorded during hypoxia and the blood oxygen dissociation curves shown in Fig. 1, it is obvious that a similar situation is occurring in both skipjack and yellowfin tunas during hypoxia.

O_2 delivery (i.e., $C_{aO_2} \times \dot{Q}$) in yellowfin tuna remained at control levels until P_{iO_2} had fallen to 50 mmHg, whereas it began to decline at a P_{iO_2} of 90 mmHg in skipjack tuna. In addition to the early decline, the fall of O_2 delivery in skipjack tuna was steeper, as evidenced by the approximately 63% drop in O_2 delivery at a P_{iO_2} of 50 mmHg compared to a 44% drop in yellowfin tuna at the same P_{iO_2} . The declines resulted from decreases in both C_{aO_2} and $\dot{Q}$.

Other fish species show equivalent declines in O_2 delivery during hypoxia. Dogfish shark show a 43% decrease at a P_{iO_2} of 80 mmHg (Short et al. 1979) and eel a 70% decline at a P_{iO_2} of 40 mmHg (Peyraud-Waitzenegger and Soulier 1989). However, the decline in O_2 delivery occurs in the former solely because of a decline in C_{aO_2} , and in the latter because of a decline in C_{aO_2} and $\dot{Q}$. Rainbow trout show no decreases in $\dot{Q}$ at P_{iO_2} levels as low as 50 mmHg (Wood and Shelton 1980). O_2 delivery, therefore, is directly proportional to C_{aO_2} which decreases by 13% at a P_{iO_2} of 90 mmHg and 38% at a P_{iO_2} of 50 mmHg (Boutilier et al. 1988). In contrast, winter flounder (*Pseudopleuronectes americanus*) make up for decreasing C_{aO_2} by increasing $\dot{Q}$ such that there is no decline in O_2 delivery at P_{iO_2} as low as 60 mmHg (Cech et al. 1977). The most relevant comparison is probably the responses of tunas and rainbow trout, since both are active, as opposed to benthic, species. C_{aO_2} decreases with hypoxia are roughly equivalent in tunas

and trout (Boutilier et al. 1988) but, because hypoxic bradycardia is not accompanied by increases in SV in tunas as it is in trout, tunas are forced to use venous reserves to support $\dot{V}O_2$ -body.

$\dot{V}O_2$ -body in yellowfin tuna remained at near-normoxic levels through a P_{iO_2} of 90 mmHg without a concurrent reduction in the venous reserve. However, skipjack tuna suffered a significant reduction in both C_{vO_2} and $\dot{Q}$ during moderate hypoxia. Although they were also able to maintain $\dot{V}O_2$ -body through a P_{iO_2} of 90 mmHg, it was at the expense of the venous reserve, as C_{vO_2} began to decrease at a P_{iO_2} of 90 mmHg. At the most severe levels of hypoxia, neither tuna species were able to supply enough oxygen to meet demand, and $\dot{V}O_2$ -body fell by about 27% in yellowfin tuna and 55% in skipjack tuna.

Of the species showing decreases in O_2 delivery (dogfish shark, eel, rainbow trout, skipjack tuna, and yellowfin tuna), only rainbow trout are able to fully counteract the decreases in O_2 delivery by reductions in C_{vO_2} (i.e., venous O_2 reserves). $\dot{V}O_2$ -total decreases 53% at a P_{iO_2} of 40 mmHg in eels and 28% at a P_{iO_2} of 80 mmHg in dogfish shark. $\dot{V}O_2$ -body ($\dot{V}O_2$ -total could not be measured at the P_{iO_2} of 50 mmHg in tunas) decreased 55% and 27% in skipjack and yellowfin tunas, respectively, at a P_{iO_2} of 50 mmHg. Rainbow trout show no change in $\dot{V}O_2$ -total down to a P_{iO_2} of <40 mmHg (Holeton and Randall 1967a).

In general, then, it appears that skipjack tuna are less hypoxia tolerant than yellowfin tuna. This conclusion is based primarily on the fact that O_2 delivery is maintained at normoxic levels through 90 mmHg in yellowfin tuna, whereas it is significantly reduced at that level in skipjack tuna. $\dot{V}O_2$ -body of both species was maintained equally well through 90 mmHg; the collapse, when it occurred, was more severe in skipjack tuna. These data also agree with those of Graham et al. (1989) who found the oxygen uptake rate of swimming albacore declined with ambient oxygen levels below P_{iO_2} of 100 mmHg.

Perhaps more important than when the collapse in O_2 delivery occurred, was how metabolism was maintained. Many of the cardiorespiratory adjustments important for maintaining arterial saturation were made at a higher P_{iO_2} in yellowfin tuna than in skipjack tuna. Improvements in $\dot{V}_E/\dot{Q}$, $\dot{V}_E/\dot{Q}$ conductance, TO_2 , and DO_2 were made at 130 mmHg in yellowfin tuna while they did not occur in skipjack tuna until P_{iO_2} had fallen to 90 mmHg. Changes that were seen first (i.e., at higher P_{iO_2}) in skipjack tuna were generally detrimental in nature. The most important, in terms of O_2 delivery, was the reduction in $\dot{Q}$ occurring at a P_{iO_2} of 90 mmHg in skipjack tuna and at a P_{iO_2} of 50 mmHg in yellowfin tuna. Because O_2 delivery to the tissues was reduced as a consequence of the lowered $\dot{Q}$, skipjack tuna were forced to maintain $\dot{V}O_2$ by drawing upon the venous oxygen reserve. In spinally blocked (i.e., non-swimming) fish, this is not critically important as metabolic rate is stable. This, however, is not the case in the wild. A reduction in activity, the common response to hypoxia in many teleosts, is not available to free-swimming tunas because they are obligate ram ventilators. Also, a common re-

sponse to hypoxia in tunas, as documented in Dizon (1977) and Bushnell and Brill (1991), is an increase in swimming speed. Skipjack tuna in moderate hypoxia will be able to meet this increased metabolic oxygen demand only by drawing further on their venous oxygen reserve. In light of the higher metabolic rate of skipjack tuna, higher minimum swimming speed, and larger increase in $\dot{V}O_2$ per increase in unit speed (Boggs 1984; Boggs and Kitchell 1991) compared to yellowfin tuna, the increased speed could not be supported aerobically for very long. However, yellowfin tuna should be able to maintain aerobic metabolism for a much longer period. The intolerance of skipjack tuna at this moderate level of hypoxia has been experimentally corroborated by Gooding et al. (1981) who found minimum oxygen tolerance level for skipjack tuna to be between 75 and 90 mmHg.

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A Bioeconomic Analysis of the Northwestern Hawaiian Islands Lobster Fishery

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Abstract Several surplus production-based bioeconomic models are applied to the Northwestern Hawaiian Islands (NWHI) commercial lobster fishery. The model which best explains the biological dynamics of the fishery is a modification of the Fox model developed by the authors. Economic costs are applied within a number of conceptual frameworks to develop the first integrated bioeconomic model of the fishery. In another development, the opportunity cost of labor based on crew share at the open access equilibrium level of fishing effort is used instead of proxy wage levels. Given the costs incurred, the fishery appears to be self-regulating in terms of long-term fishing effort for maximum sustainable yield.

Keywords Biological production models, fisheries economics, fisheries management, spiny lobster, slipper lobster.

Introduction

The Northwestern Hawaiian Islands (NWHI) lobster fishery is relatively unusual amongst the world's lobster fisheries being a distant-water fishery landing predominantly a frozen tailed product. For the first twelve years of its utilization (1977-1988), laissez faire conditions predominated with a minimum of biological regulation. However in 1989, problems of over-capacity were not resolved through voluntary exit of marginal producers, and the growth of Hawaii's commercial longline fisheries posed the possibility of short-term entry by additional vessels. As a result, proposals were circulated to implement limited entry into the NWHI lobster fishery, and interest was raised in determining the optimal level of harvest.

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The fishery has been actively regulated and monitored only since 1983, thus providing a very short time-series of data for modeling the biological population dynamics. Similarly, fishing vessel operations in the NWHI lobster fishery and in alternative fisheries have not been stable, with substantial switching between fisheries. As a result, some of the statistical grounds for modeling the fishery appear weak. On the other hand, interest in developing a more refined management system for this fishery is growing, suggesting that even a preliminary model of the fishery would be valuable as a benchmark for evaluating alternative management measures. The empirical results of these models are surprisingly robust.

Two questions this study addresses are: a) what is the appropriate biological model to use for bioeconomic purposes in this fishery, and b) given a relatively new fishery, what are the implications of the choice between models? Clearly the period of time in which the NWHI lobster fishery has been prosecuted precludes a full test of the alternative surplus production model we develop in this paper. We have attempted to do this in another context (Yoshimoto and Clarke, *in press*). On the other hand, fishery management is an immediate and on-going process. In lieu of an integrated bioeconomic modeling approach to the problem, fishery managers are left with a number of discrete pieces of information on the fishery management problem but with no overall perspective on the potential range of alternative solutions to that problem. We believe one advantage of surplus production bioeconomic models is the use of limited information to provide such guidance. Obviously the results need to be tempered by a flexible and adaptive approach to management actions.

This paper presents the first full bioeconomic model of the NWHI lobster fishery. After a brief historical summary of how the fishery developed, we begin with the derivation of biological and economic production functions. Four established surplus production models along with a new refinement to a previously accepted model are used in developing a bioeconomic analysis of the fishery. Biological parameters are estimated from a limited time series of annual fishery-wide catch and effort data, then combined with price and cost information to construct the bioeconomic models. The third part of the paper compares the models. The fourth and fifth parts summarize the results of the bioeconomic models and their implications for the NWHI lobster fishery. Finally, we present some thoughts on the use of alternative biological surplus production models on management strategy.

Background

Commercially viable concentrations of the spiny lobster *Panulirus marginatus* (henceforth referred to as spiny lobster) were discovered in the 1970s in the NWHI (Fig. 1), a group of islands, banks, and reefs extending 1,200 nautical miles northwest of the main Hawaiian Islands (Uchida and Tagami, 1984). Almost immediately, a commercial trapping fishery for live spiny lobster developed in Hawaii and grew rapidly to include 10 vessels, which in 1981 landed 350 metric tons (t) with an ex-vessel value of \$2.7 million. By 1982, the Honolulu market was unable to absorb this relatively large volume of live lobster, ex-vessel prices dropped, and the fleet contracted. At that time, some vessels began processing spiny lobster at sea and landing frozen tails, allowing access to the worldwide market for frozen lobster tails. Thereafter, vessel operators began expanding their

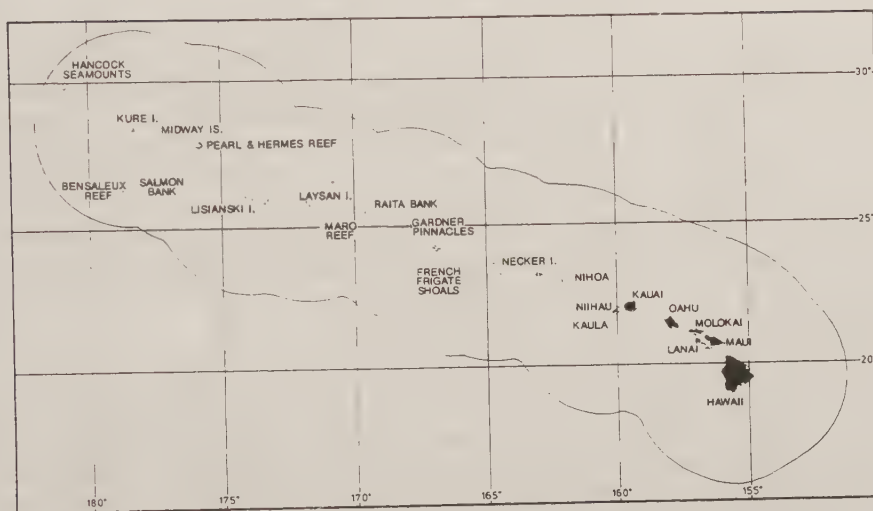


Figure 1. Hawaiian Islands with the Northwestern Hawaiian Islands demarcated by 161 degree west longitude.

efforts, and the fishery grew rapidly. Sixteen vessels participated in the NWHI lobster fishery in 1985, the same year vessel operators began targeting and landing significant quantities of the slipper lobster *Scyllarides squammosus*, which had been an incidental catch.

By 1986, the NWHI had the largest slipper lobster fishery in the United States, and its spiny lobster landings were second only to Florida's: combined landings had jumped to 1,000 t; ex-vessel revenue exceeded \$6 million. Having developed into an industrial, multispecies lobster fishery, it was composed of medium- to large-sized fishing vessels (62–110 ft) traveling long distances and fishing for extended periods (Clarke and Pooley, 1988). However, entry and exit patterns showed considerable turnover in vessel participation in the fishery.

The NWHI lobster fishery originally operated under State of Hawaii regulations, but in March 1983, a federal fishery management plan (FMP) prepared by the Western Pacific Regional Fishery Management Council was implemented with the objective of protecting the reproductive spawning biomass. Initially, the FMP regulated only the spiny lobster fishery, but it was amended in 1987 to include slipper lobster. Regulations included minimum sizes, escape-vented traps, and returning berried females. Fishing effort was not restricted, except in a few areas declared off-limits as marine mammal and sea bird refugia.

From a purely biological perspective, the NWHI lobster fishery presented a unique situation in which fishery managers had relatively good estimates of the pre-exploitation condition of spiny lobster stocks based on the exploratory research surveys which preceded the commercial fishery. These initial surveys allowed for comprehensive biological assessments of the spiny lobster fishery as it developed (Uchida and Tagami, 1984; Polovina, 1989a). However, complications in monitoring the fishery quickly arose as the commercial fishery developed new gear configurations and as the importance of the slipper lobster landings grew. By 1986, effort levels appeared to be biologically excessive (Polovina *et al.*

1987), and several economic studies were initiated by the Honolulu Laboratory and the Council to examine management implications. But as fishing intensity stabilized, interest waned in managing the fishery through economic regulation until an apparent recruitment (or catchability) crisis late in 1989. The Crustacean FMP was amended in 1991 to limit entry into the fishery based on current levels of participation, and a flexible fishing season based on an annual quota was proposed for 1992. Economic optimization of the fishery has not really been considered; the limited entry and seasonal regulations are pragmatic and oriented toward preserving a threshold spawning biomass in the fishery (Polovina, 1991).

Methods

Production Models

Five models with distinctly different biological production relationships are assessed for their applicability to the NWHI lobster fishery: the Schaefer (1957) model, the Fox (1970) model, the Schnute (1977) modification of the Schaefer model, a threshold-type model as presented by Sathiendrakumar and Tisdell (1987), and our modified version of the Fox model. Hereafter, for the sake of brevity the models will be referred to as the Schaefer, Fox, Schnute, Threshold, and CY&P, respectively. They consist of three distinctly different production (*i.e.*, yield and effort) relationships: The Schaefer and Schnute models have a parabolic or logistic relationship, the Fox and CY&P models follow a Gompertz curve (Richards, 1959), and the Threshold model has a logarithmic curve that asymptotically approaches a maximum.

The Schaefer, Fox, Schnute, and CY&P models relate stock size, fishing effort, and yield to one another. Stock size adjusts to different levels of effort, and sustainable yield is a result of applied effort. As will be shown later, the yield-effort relationships can be quite different in terms of predicted results. The Fox model has had reasonable results when used for other lobster fisheries (Campbell and Hall, 1987; P. Breen, personal communication 1989). To our knowledge, the Threshold model has not previously been used for a lobster fishery. The Schnute model was applied by Polovina (1989b) to a system of simultaneous production relationships for forecasting in the NWHI lobster fishery. He estimated individual bank parameters using area-by-area catch and effort data and pooling the area results for a fishery-wide model.

The five models in our study are fit from the same NWHI logbook data used by Polovina (1989b), but catch and effort are pooled for the entire NWHI fishery.¹ We feel this more closely approximates economic considerations in the fishery. Vessel operators frequently fish various banks during a trip, and the decision to make a trip is not based on the average annual or seasonal productivity of any individual bank.

The generalized stock production model (Pella and Tomlinson, 1969) is

¹ Whether bank-by-bank or fishery-wide analysis is appropriate biologically is a matter of concern. Some aspects of recruitment are clearly fishery-wide (*e.g.*, the circulation of lobster phyllosomes throughout the archipelago) while others are bank-specific (*e.g.*, settling out of larvae). Polovina (1991) found the CY&P model applied to fishery-wide data was consistent with bank-by-bank analysis.

$$dX/dt = rX - (r/K)X^m - C; \quad (1)$$

where dX/dt is the growth rate of biomass; r , the intrinsic growth; C , the catch rate; X , the current biomass; and K , the maximum stock level or virgin biomass. When $m = 2$, then

$$dX/dt = rX(1 - X/K) - C, \quad (2)$$

and the growth rate is of the logistic form. When $m \rightarrow 1$, then

$$dX/dt = rX \ln(K/X) - C, \quad (3)$$

and the growth rate follows a Gompertz curve (cf. Richards, 1959). The basic difference between the logistic and Gompertz curves is that the logistic is symmetrical while the Gompertz is not, implying, in an extreme case, the potential extinction of the fishery. Using the assumption of $C = qEX$, where E is the rate of fishing effort, q is the catchability coefficient, and catch per unit effort (CPUE) is defined by $U = C/E$, current biomass is given by $X = U/q$. The resulting biomass equation can then be used to convert Equations 2 and 3 into forms directly applicable to annual catch and effort data. With the Pella and Tomlinson (1969) method, an iterative procedure was tested to determine which value of m best fits Equation 1. However, the true value of m could not be estimated from the data on the NWHI lobster fishery because several quite different m values produce equivalently good fits. The R statistic, a measure of improved fit compared to reliance on the mean catch as the parameter value, is >0.98 for m values covering the range of those used in these production models: 2.0 (Schaefer), 1.01 (Fox), and 0.01 (Threshold). The fact that the true value of m could not be estimated with the Pella and Tomlinson model is probably due to the relatively short time series of data available (P. Tomlinson, personal communication 1990).

Two models use the finite difference approximation $dU/dt \approx (\bar{U}_{n+1} - \bar{U}_{n-1})/2$, where $\bar{U}_n$ is the average CPUE for a given year, n (— denotes the mean):

$$\text{Schaefer: } (\bar{U}_{n+1} - \bar{U}_{n-1})/(2\bar{U}_n) = r - (r/(qK))(\bar{U}_n) - q(\bar{E}_n), \quad (4)$$

$$\text{Fox: } (\bar{U}_{n+1} - \bar{U}_{n-1})/(2\bar{U}_n) = r \ln(qK) - r \ln(\bar{U}_n) - q\bar{E}_n, \quad (5)$$

where $\bar{E}_n$ is the total effort expended in year n . The parameters r , q , and K are estimated by ordinary least squares (OLS) with a time series of catch and effort data.²

² It would be useful to compare our estimates of K with pre-exploitation or fishery-independent measures of biomass. Unfortunately, comparable estimates of pre-exploitation biomass are not readily available because the gear used in early research cruises failed to sample slipper lobster. Polovina and Tagami (1979) estimated spiny lobster populations for a subsection of one of the banks (Necker Island) using depletion methods. Uchida and Tagami (1984) extrapolate those results and report a NWHI wide spiny lobster MSY range of between 210,000 and 435,000 lobsters above 8.25 centimeter carapace

Many bioeconomic studies incorporate biological parameters that have been estimated by the Schaefer and Fox models. Although some authors (*e.g.*, Uhler, 1980) suggest that finite difference models may be useful for economic analysis, others (*e.g.*, Schnute, 1977) have shown these models to be invalid for non-equilibrium conditions and have suggested that modified versions be applied to better represent the dynamic nature of fishery yield and effort interactions. Schnute (1977) argues that a major problem with the Schaefer and Fox models is that they can predict next year's CPUE without specifying next year's anticipated effort, contradicting almost all theory on fisheries biology. Another problem involves the finite difference approximation, which assumes that CPUE is linear over the course of a given year. Based on a review on monthly CPUE data from the NWHI lobster fishery (Clarke *et al.* 1987), this assumption is questionable. Thus, the Schaefer and Fox models are presented for comparison purposes only, while the Schnute, Threshold, and CY&P models are explored in greater detail in our paper.

Schnute (1977:594) developed a modified version of the Schaefer model using an integration procedure:

$$\begin{aligned} \text{Schnute: } \ln(\bar{U}_{n+1}/\bar{U}_n) = & r - (r/(qK)) (\bar{U}_n + \bar{U}_{n+1})/2 \\ & - q(\bar{E}_n + \bar{E}_{n+1})/2. \end{aligned} \quad (6)$$

For the CY&P model, we follow Schnute's lead and apply a similar approach to the Fox model, using a Taylor approximation (derivation in Appendix A):

$$\begin{aligned} \text{CY\&P: } \ln(\bar{U}_{n+1}) = & (2r/(2+r))\ln(qK) + ((2-r)/(2+r))\ln(\bar{U}_n) \\ & - (q/(2+r))(\bar{E}_n + \bar{E}_{n+1}). \end{aligned} \quad (7)$$

By using OLS, the three constants can be estimated from Equation 7 by

$$\ln(\bar{U}_{n+1}) = c_1 + c_2 \ln(\bar{U}_n) + c_3(\bar{E}_n + \bar{E}_{n+1}); \quad (8)$$

where $r = 2(1 - c_2)/(1 + c_2)$, $q = -c_3(2 + r)$, and $K = e^{c_1(2+r)/(2r)/q}$. The CY&P model incorporates the same nonlinear assumptions as in the Schnute model, and, as will be demonstrated, has a good fit to the NWHI commercial lobster fishery's limited time series data.

The Threshold model presents an interesting twist in the conventional yield-effort relationship. Unlike the previous models for which stock size varies with effort, the Threshold model shows decreasing returns to effort after reaching a critical level. This can be interpreted either as the result of competition among vessels or long-term population adjustments (Sathiendrakumar and Tisdell, 1987).

The Threshold model shows catch reaching its maximum asymptotically, expressed as $C = A - Be^{-kE}$, where C is catch and E is effort. The parameters A , B , and k can be estimated with the transformation

length. However the minimum size limit actually implemented was smaller: since the inception of Federal management a legal-sized spiny lobster equates to approximately 7.7 centimeters carapace length while the legal slipper lobster size equates to an 8.3 centimeter carapace (actual regulation is now by tail width).

$$\ln(A - \bar{C}_n) = \ln(B) - k\bar{E}_n; \quad (9)$$

where $\bar{C}_n$ is the total catch, $\bar{E}_n$ is the total effort for year n , and A corresponds to the maximum catch or threshold level of catch.³ Although not specified by the original authors, we interpret k as the catchability coefficient and B as virgin biomass. With a method similar to that employed by Sathiendrakumar and Tisdell (1987), a value for A is chosen that is slightly higher than the highest combined catch levels recorded for each species of lobster. The initial value of A is then changed iteratively until the regression of $\ln(A - C)$ against E gives the best fit in terms of maximizing R^2 . The Threshold model has been used for tunas that are exploited over only a portion of their range, but it seems applicable to a benthic fishery as well. It can be applied to lobster stocks in the NWHI because not all of the lobster population is subject to exploitation throughout the year. At certain times of the year, lobster are less vulnerable to trapping because of environmental effects (*e.g.*, sea state, water temperature) on behavioral activity, such as nightly foraging (Karnofsky and Price, 1989). Finally, minimum size regulations and escape vents limit the fishable proportion of the total population.

Catch and Effort Data

The basic unit of fishing effort in the NWHI lobster fishery is the trap-haul, and all vessels currently participating in the fishery use black, plastic traps made by one manufacturer. Bait and general fishing methods are also homogeneous throughout the fleet, and although differences between vessels do exist, all trap-hauls are assumed to be equally efficient for this analysis.

Catch and effort data for 1982–1989 are presented in Table 1. Length-frequency information taken from research sampling has been used to adjust 1982–1987 slipper lobster categories to account for the implementation of management regulations in 1988.⁴ Catch per trap-haul for the two species has been combined into one unit stock because the targeting practices of fishermen are not known and the habitat of the two types of lobster overlap.⁵

Price

The revenue function is created by applying Hawaii's 1986–1988 average ex-vessel lobster price, adjusted for inflation, to the biological production functions.

³ At low levels of effort (E), the Threshold model can predict negative catch levels (C). This is not a problem at reasonable effort levels. In an alternative specification, where $A = B$, the Threshold model is non-linear.

⁴ Spiny lobster, the initial target species of the fishery, are reported in catch and effort logs as either legal, sublegal, or berried (egg-bearing females). These categories are also used for slipper lobster catches, which the fishermen voluntarily reported prior to their management in 1988.

⁵ The post-settlement growth rates of the two lobsters are similar reaching minimum legal size at 3.1 and 3.3 years, respectively, for the spiny and slipper lobster (Polovina and Moffitt, 1989). The habitat for the two species generally overlaps in that spiny lobster are normally concentrated in waters 15–25 fathoms while slipper lobster concentrate at slightly deeper depths of 20–30 fathoms. Nonetheless the two species show no definite delineation by depth, and it is not possible to segregate effort by species from the catch and effort reports submitted by fishermen. The problem of modeling these two species with one production model has been raised repeatedly in the past two years, but no solution has been found.

Table 1
Number of Lobster Retained, Fishing Effort (Number of Trap-Hauls), and Average Catch Per Unit Effort (CPUE) in the Northwestern Hawaiian Islands Lobster Fishery, 1982–1989

Year	Retained Lobster			Effort (in Trap-Hauls)	CPUE
	Spiny Lobster	Slipper Lobster	Combined Total Lobster		
1982 ^a	—	—	148,214	47,738	3.10
1983 ^b	210,100	24,600	234,700	84,870	2.77
1984	667,300	205,100	872,400	363,024	2.40
1985	956,000	856,700	1,812,700	983,062	1.84
1986	896,400	891,000	1,787,400	1,352,580	1.32
1987	394,600	343,200	737,800	804,723	0.92
1988	889,000	168,600	1,057,600	845,200	1.25
1989	944,100	216,200	1,160,300	1,071,538	1.08

Note: The 1983–1986 data are from Clarke *et al.* (1987); 1987–1989 data are from Landgraf *et al.* (1990).

^a The 1982 catch is estimated from weight of lobster landed; effort is estimated by back-extrapolating using 1983 levels of reported trapping intensity (where 1982 trap-hauls per trip are 75% of the number of trap-hauls per trip in 1983) and multiplying by the number of trips ($n = 19$) reported for that year.

^b The 1983 data are extrapolated from 9 months of actual data to account for the entire year.

Real ex-vessel prices (in U.S. dollars) for Hawaii's spiny and slipper lobsters, calculated on a whole weight basis from nominal revenue data, adjusted for inflation to 1989 price index levels, are shown in Table 2 for 1982–1989 (Landgraf *et al.* 1990). The real (1988 base year) weighted average price of combined spiny and slipper lobsters was \$4.55 per lobster for 1986–1988, the period for which detailed cost and effort data were available.

During the last 5 years, 95% of the lobster landed (by weight) from the NWHI have been frozen tails (Landgraf *et al.* 1990). Although some of them are sold locally to Hawaii's seafood wholesalers, most are transshipped to the U.S. main-

Table 2A
Average Nominal and Real^a Ex-Vessel Price^b per Pound (Round Weight) of Combined Spiny and Slipper Lobster, Pounds Landed, and Nominal and Real Total Revenue^b in the Northwestern Hawaiian Islands Lobster Fishery, 1982–1989

Year	Price per Pound		Round Weight	Revenue	
	Nominal	Real		Nominal	Real
1982	3.60	4.78	187,000	673,000	893,401
1983	2.91	3.76	203,000	591,000	762,366
1984	2.58	3.22	1,017,000	2,624,000	3,279,079
1985	2.49	2.94	2,368,000	5,887,000	6,951,504
1986	2.72	3.14	2,202,000	5,982,000	6,907,832
1987	4.12	4.52	969,000	3,988,000	4,383,351
1988	3.56	3.69	1,405,000	5,000,000	5,187,290
1989	4.28	4.28	1,470,000	6,291,000	6,291,000

^a Adjusted for inflation to 1989 Honolulu consumer price index levels.

^b In U.S. dollars.

Table 2B
Average Nominal and Real^a Ex-Vessel Price^b and Number of Combined Spiny and Slipper Lobsters Landed in the Northwestern Hawaiian Islands Lobster Fishery, 1982–1989

Year	Price per Lobster		Number
	Nominal	Real	
1982	4.54	6.03	148,214
1983	2.52	3.25	234,700
1984	3.01	3.76	872,400
1985	3.25	3.83	1,812,700
1986	3.35	3.86	1,787,400
1987	5.41	5.94	737,800
1988	4.73	4.90	1,057,600
1989	5.42	5.42	1,160,253

^a Adjusted for inflation to 1989 Honolulu consumer price index levels.

^b In U.S. dollars per lobster.

land and compete with other worldwide sources of lobster for the U.S. market share. Landings of NWHI spiny and slipper lobsters account for <1% of the worldwide lobster production and only 20% of U.S. production (Samples and Gates, 1987). Therefore, NWHI fishermen are considered price takers in the international lobster market, and supply interaction with demand is excluded from our analysis.

Cost of Effort

Determining the economic cost of fishing effort can be a difficult process because bioeconomic models are constructed to indicate the optimum social investment in a fishery over the long run, while firm costs usually are viewed as short-run phenomena. Our paper follows the usual microeconomic and bioeconomic assumptions of a competitive market economy in which factor markets are in equilibrium and maximization of profits (net revenue) is the firm's decision criterion. Costs should reflect social opportunity costs (following Anderson, 1982). Pragmatically, where there is information on average private costs (as is the case for the NWHI lobster fishery), private costs closely approximate the social costs (Anderson, 1982):

$$TC \approx c * E;$$

where *TC* is the total cost (per trap-haul); *c*, average cost (per trap-haul); and *E*, effort (in trap-hauls). Cost per trap-haul should be chosen at the point which approximates the minimum point on the long-run average cost curve, *i.e.*, the point of long-run industry equilibrium (ignoring biological effects). This can then be assumed to be constant, which does not significantly affect the results (Anderson, 1982).

The cost of effort for the bioeconomic model can be estimated in two ways: average fleet costs, which combine the costs from the three vessel classes com-

prising the fleet, or "optimal" costs, which are derived from the vessel class (*i.e.*, Class II) that appears to be best suited for this fishery (Clarke and Pooley, 1988).⁶ The unweighted average fleet cost per trap-haul was \$4.60 over the 3 years for which detailed cost and operating information was available (1986–1988), compared with \$3.48 for the Class II vessels (the vessel class with the lowest cost per trap-haul). We consider the latter to be the basic social opportunity cost of fishing effort. However, this cost should be adjusted for imperfections in the labor market in order to represent the long-run opportunity cost of lobster fishing.

The NWHI lobster fishery is a small component of Hawaii's economy and can be viewed as a price taker for most inputs. Within any individual fishing trip, extending fishing effort may increase marginal costs, but entry and exit patterns of this fishery and variation in trip duration indicate that the flexibility of productive inputs is sufficient to view operating and vessel costs per unit effort as constant. Furthermore, since lobster boats represent mobile capital capable of shifting between different fisheries (*e.g.*, Hawaii's longline fishery or the Pacific Northwest's crab fisheries), the opportunity cost of capital is reflected by the annualized market value of the vessels.

Only for labor does Hawaii's input market seem distorted for NWHI lobster fishing vessels. Labor payments in commercial fishing are outside normal employment practices, and conditions on the NWHI lobster fishing vessels are outside the norm of other fishing fleets in Hawaii. As a result, a number of NWHI lobster fishing vessel captains have had to hire crews from the Pacific Northwest and pay for their transportation to and from Hawaii. This poses a substantial problem for calculating the opportunity cost of labor since there is no truly comparable competitive labor market. Commercial fishing crews give up a certain income and take on a particular way of life in hopes of receiving a portion of the economic rents from the fishery and the profits of individually efficient producers. (In 1986, crew members on larger lobster boats received \$148 per fishing day, while crew shares on the midsized boats ranged from \$126 for efficient producers to \$79 for inefficient producers.) The opportunity cost of labor for commercial fisheries has been calculated a number of different ways (Anderson, 1977; Clark, 1985). Clarke and Pooley (1988) argued that it is inappropriate to use manufacturing wage rates as proxies for the opportunity cost of labor on lobster boats because there is no occupational equivalent to distant-water commercial fishing. Instead, labor cost should be determined from the crew share at a point where the fleet appears to be in open access equilibrium (OAE), *i.e.*, where there are no rents. This can be viewed as the value of the marginal product of labor in which no resource rents are accruing to the crew (or the vessel).

Cost-earnings data indicated the fleet was breaking even in 1986, with an

⁶ A cost-earnings study (Clarke and Pooley, 1988) on the economic performance on the NWHI lobster fleet for 1986 revealed varying rates of return on lobster operations. Vessels were classified according to their physical and operational characteristics, and while certain sectors of the fleet showed a positive return on investment, overall the fleet returned \$–198,000 on \$6.214 million total revenue in 1986.

The vessel cost portion of the study included estimates on fixed and variable costs for all of the classes. Fixed costs included estimated capital costs (10% of investment) and annual repair, vessel insurance, administrative, and loan (interest payment) costs. Operating costs included all trip costs and crews and captains' shares. Vessel depreciation was fixed at 4% but included a supplemental component if annual vessel repair was less than 10% of depreciation.

average labor cost of \$137.00 per crew member per fishing day (Clarke and Pooley, 1988). This labor cost represents a wage rate of approximately \$10.00 per hour for 16-hour fishing days, substantially less than Hawaii's contract construction rate of \$17.42 per hour in 1986 but about the same as the manufacturing wage rate of \$8.86 per hour. Recalculating vessel operating costs (Table 3) with this labor cost provides the cost figure used in the remainder of our study: \$2.97 per trap-haul, the minimum long-run average cost during a period of intensive fishing.

Bioeconomic Models

At a static equilibrium, dX/dt equals zero, and equations relating catch and effort can be obtained for the Schaefer and Schnute models

$$C = qKE(1 - qE/r), \quad (10)$$

and for the Fox and CY&P models

$$C = qKEe^{-qE/r}. \quad (11)$$

Once the yield-effort equations are established for the various models, reference points important for evaluating anticipated or predicted fishing effort can be determined by incorporating cost and revenue data. The economic portion of the bioeconomic models, as proposed by Gordon (1954), assumes constant price (p) for lobster and cost (c) for each unit of effort (or trap-haul), where revenue equals pC and total cost equals cE . The relationship between cost and revenue implies, that at OAE, biomass $\bar{X}$ is $c/(pq)$ (Clark, 1985).

Static OAE or maximum economic yield (MEY) disregards the difference between present and future values of funds. The idea behind MEY is that the fishery is managed as a capital good maximizing net present value (Clark, 1985). The equation to solve for optimal biomass (X^*) under discounting is

$$G'[X^*] - \frac{c'[X^*] G[X^*]}{p - c[X^*]} = \delta; \quad (12)$$

Table 3
Cost per Trap-Haul^a for the Northwestern Hawaiian Islands Lobster Fishery, 1986–1988

Cost Category	Cost per Trap-Haul		
	1986	1987	1988
(1) Fleet average	4.99	4.51	4.29
(2) Minimum (Class II)	3.40	3.53	3.52
(3) Labor opportunity cost adjustment (Class II)	3.53	3.04	2.97

^a Calculated in U.S. dollars as (1) fleet average cost, (2) minimum cost for Class II vessels (most efficient), and (3) labor opportunity cost-adjusted minimum cost per trap-haul when opportunity cost of labor is at open access equilibrium levels of fishing effort.

where $G[X]$ is the natural growth rate of lobster biomass (X), δ is the real annual discount rate, and $c[X] = c/(qX)$ is the cost of catching one unit of biomass when the present biomass is X .

In the Schaefer and Schnute models, as specified by Clark (1985),

$$G[X] = rX (1 - X/K), \quad (13)$$

and for the Fox and CY&P models,

$$G[X] = rX \ln(K/X). \quad (14)$$

Optimal biomass can be determined in the logistic model by

$$X^* = \frac{1}{4} \left(\bar{X} + K \left(1 - \frac{\delta}{r} \right) + \sqrt{\left(\bar{X} + K \left(1 - \frac{\delta}{r} \right) \right)^2 + \frac{8K\bar{X}\delta}{r}} \right). \quad (15)$$

Optimal biomass for the Gompertz model can be determined iteratively by

$$\ln \left(\frac{K}{X^*} \right) - \left(1 + \frac{\delta}{r} \right) \left(1 - \frac{\bar{X}}{X^*} \right) = 0, \quad (16)$$

which was derived from Equations 12 and 14 by using elementary calculus. Once the values for optimal biomass have been determined for an appropriate range of discount rates, then optimal yield ($G[X^*]$) and optimal effort (E^*) can be determined by

$$E^* = \frac{G[X^*]}{qX^*}. \quad (17)$$

For the Threshold model, the natural growth rate G cannot be expressed explicitly in terms of X^* . Instead, E^* is determined from a modification of Equation 12 (Appendix B). Our derivation involves an iteration of E^* instead of X^* , with E^* determined iteratively from the equation

$$\frac{k}{\frac{kE^*}{G[E^*]} - \frac{1}{A - G[E^*]}} + \frac{c}{p - \frac{cE^*}{G[E^*]}} = \frac{\delta G[E^*]}{q(E^*)^2}, \quad (18)$$

where

$$G[E^*] = A - B e^{-kE^*}. \quad (19)$$

The catchability coefficient q is assumed to be k in the Threshold model.

Results

The Schaefer, Schnute, Fox, and CY&P production models are estimated using OLS with 1982-1989 catch and effort data (from Table 1):

Schaefer:

$$(\bar{U}_{n+1} - \bar{U}_{n-1})/(2\bar{U}_n) = 0.672 - 0.277 \bar{U}_n - 4.66 \times 10^{-7} \bar{E}_n.$$

$$t\text{-statistic} \quad (2.62) \quad (-3.02) \quad (-3.18)^*$$

$$R^2 = 0.78 \quad R^2\text{-bar} = 0.64 \quad DW = 2.01 \quad D\text{-h} = -0.00644^*$$

Schnute:[#]

$$\ln(\bar{U}_{n+1}/\bar{U}_n) = 1.43 - 0.512(\bar{U}_n + \bar{U}_{n+1})/2 - 9.13 \times 10^{-7}(\bar{E}_n + \bar{E}_{n+1})/2.$$

$$t\text{-statistic} \quad (4.75)^{**} \quad (-5.25)^{**} \quad (-5.01)^{**}$$

$$R^2 = 0.90 \quad R^2\text{-bar} = 0.84 \quad DW = 3.04 \quad D\text{-h} = -1.31^*$$

Fox:

$$(\bar{U}_{n+1} - \bar{U}_{n-1})/(2\bar{U}_n) = 0.312 - 0.390 \ln(\bar{U}_n) - 3.76 \times 10^{-7} \bar{E}_n.$$

$$t\text{-statistic} \quad (1.77) \quad (-2.48) \quad (-2.55)$$

$$R^2 = 0.71 \quad R^2\text{-bar} = 0.52 \quad DW = 1.80 \quad D\text{-h} = 0.266^*$$

CY&P:[#]

$$\ln(\bar{U}_{n+1}) = 0.583 + 0.437 \ln(\bar{U}_n) - 2.80 \times 10^{-7}(\bar{E}_n + \bar{E}_{n+1}).$$

$$t\text{-statistic} \quad (4.37)^* \quad (4.49)^* \quad (-4.92)^{**}$$

$$R^2 = 0.98 \quad R^2\text{-bar} = 0.97 \quad DW = 2.92 \quad D\text{-h} = -1.16^*$$

$$* P = 0.05$$

$$** P = 0.02$$

$$^{\#} = 1 \text{ iteration of Cochrane-Orcutt procedure for serial correlation.}$$

All models, with the exception of the Fox, have coefficients with the proper signs and *t*-statistics significant at the 5% level or better. The Durbin-Watson test for autocorrelation was applied, but the number of observations is insufficient to determine whether a significant problem exists (Pindyck and Rubinfeld, 1981).

Therefore we applied the Durbin h test to the Schaefer and Fox models and the results support the null hypothesis of zero first-order autocorrelation. The Durbin h -statistic detected autocorrelation in the Schnute and CY&P models. The Cochran-Orcutt procedure (Wittink, 1988) was applied as a correction to these models (Table 4a).

The highest reported catch level for each individual species (Table 1)—1.85 million combined spiny and slipper lobsters—is used initially for A in the Threshold model. Iteration of A to maximize R^2 fails to converge to a value that we believe is realistic for the fishery. Therefore, A is increased iteratively until the improvement in the R^2 value is only 1% as proposed by Sathiendrakumar and Tisdell (1987).

The Threshold model of the NWHI lobster fishery is estimated as

$$\ln(1,900,000 - C) = 14.62 - 1.85 \times 10^{-6} E.$$

$$t\text{-statistic} \quad (27.0)^{****} (-2.82)^*$$

$$* \quad P = 0.05$$

$$**** \quad P < 0.001$$

This can be rewritten as $C = 1,900,000 - e^{(14.62 - 0.00000185E)}$, with k equal to 1.85×10^{-6} and B equal to 2,233,112.

Estimates of parameters r , q , and K for each model are given (Table 4a) along with statistics showing the relative fit of these models to the time series data. Because of the complex structure of the four models, exact variances of K could not be obtained, and therefore the standard deviations of the alternative estimates of MSY could not be calculated. Standard deviations of r , q , K , MSY and effort

Table 4A
Values of Parameters Estimated by the Schaefer, Schnute, Fox, CY&P, and Threshold Models for the Northwestern Hawaiian Islands Lobster Fishery

Parameter	Schaefer	Fox	Schnute	CY&P	Threshold
r	0.67	0.39	1.43	0.79	—
q	4.66×10^{-7}	3.76×10^{-7}	9.13×10^{-7}	7.83×10^{-7}	—
k	—	—	—	—	1.85×10^{-6}
K	5,220,226	5,918,398	3,050,615	3,574,015	—
B	—	—	—	—	2,233,112
A	—	—	—	—	1,900,000
R^2	0.78	0.71	0.90	0.98	0.57
R^2_{adj}	0.64	0.52	0.84	0.97	0.50
D-W ^a	2.01	1.80	3.04	2.92	1.09
Durbin h	-0.006**	0.27**	-1.31**	-1.16**	—
df	3	3	3	3	6

** No serial correlation at 5% level.

^a Not sufficiently sensitive with $n = 6$.

r = intrinsic growth in year⁻¹.

q = catchability in trap-hauls⁻¹.

k = Threshold catchability in trap-hauls⁻¹.

K = maximum biomass in number of legal lobsters.

B = Threshold virgin biomass in number of legal lobsters.

A = Threshold catch estimate in number of legal lobsters.

at MSY were obtained from bootstrapping (Efron and Tibshirani, 1986) using the Shazam statistical package (White *et al.* 1990). Sampling with replacement was applied to the residuals of the regression used to test each model and a bootstrap sample was created. Another regression was then performed on the bootstrap sample which provided new estimates of r , q , K , MSY, and effort at MSY. This procedure was performed a thousand times and the mean, standard deviation, and coefficient of variation of each parameter were calculated (Table 4b). Based on the coefficients of variation, instability was found in MSY for the Schnute model and in parameter K and effort at MSY for the Fox and Schnute models. Although the CY&P and the Schaefer models performed well, the results should be tempered because of the small sample size.

The yield-effort curves for all five models are shown in Figure 2. The inclusion of price and cost information in the production equations for the Schnute, CY&P, and Threshold models is depicted in Figure 3, along with the relative positions of MEY and OAE effort levels.

The four non-asymptotic models (Schaefer, Fox, Schnute, and CY&P) predict

Table 4B

Means, Standard Deviations (STD) and Coefficients of Variation (CV) of the Bootstrap Estimates ($n = 1000$) of Parameters r , q , K , MSY and Effort at MSY in the Schaefer, Schnute, Fox and CY&P Models for the Northwestern Hawaiian Islands Lobster Fishery

Model	Parameter	Mean	STD	CV
CY&P	r	0.94	0.37	0.40
	q	9.19×10^{-7}	3.63×10^{-7}	0.39
	K	3,545,500	1,391,800	0.39
	MSY	1,069,500	170,750	0.16
	E(MSY)	1,058,700	341,180	0.32
Schnute	r	1.40	0.63	0.45
	q	9.13×10^{-7}	3.72×10^{-7}	0.41
	K	1,537,800	75,924,000	49.37
	MSY	1,172,300	4,459,000	3.80
	E(MSY)	818,880	2,214,000	2.70
Fox	r	0.39	0.16	0.41
	q	3.80×10^{-7}	1.48×10^{-7}	0.39
	K	6,373,500	9,783,000	1.53
	MSY	845,530	495,410	0.59
	E(MSY)	1,012,000	1,587,500	1.57
Schaefer	r	0.67	0.26	0.39
	q	4.65×10^{-7}	1.50×10^{-7}	0.32
	K	5,716,100	2,309,100	0.40
	MSY	854,070	190,360	0.22
	E(MSY)	714,720	143,440	0.20

r = intrinsic growth in year⁻¹.

q = catchability in trap-hauls⁻¹.

K = maximum biomass in number of legal lobsters.

MSY = maximum sustainable yield in number of legal lobsters.

E(MSY) = fishing effort in trap-hauls at MSY level of production.

MSY within a 22% range for this fishery (Table 5). Effort levels at MSY are predicted within a 30% range for the four models, while estimated profits at MSY vary 70% because of differences in predicted effort. Predictions of MSY for the Threshold model are not relevant because the model uses an asymptotic maximum.

The five models show considerable differences in predicted optimums, *i.e.*, MEY and effort. The MEY varies by as much as 54% while corresponding effort varies by as much as 47%. Profit at MEY varies by 60%. Large differences also exist between the Threshold and other models for predicted yield at OAE. The Threshold model predicts a yield almost three times that of the Schaefer model, whereas the non-asymptotic models estimate both yield and effort levels within 28%. These substantial differences demonstrate clearly the importance of model choice.

Discounted optimal values for Y^* , E^* , X^* , and U^* , along with estimates of resource rent ($TR - TC$, where TR is total revenue) are shown in Table 6. The discount rates are representative of biological considerations (1% and 5%), social accounting (10%), and private interest rates compounded by risk (25%) (Clark 1985). Model results at 0% (no discounting) and ∞ confirm values estimated for static MEY and OAE (Table 5). All models show the same trends over the relevant range (i between 0% and 25%) although absolute values vary. On a percentage basis, estimated optimal effort values vary the most over alternative interest rates within a model (5–24%), while estimated resource rents (*i.e.*, estimated profit, not including consumer and producer surpluses) vary the least (0–7%). The MEY varies most in the Fox model (11%) and least in the Threshold model (2%). Optimal biomass levels and optimal catch per trap-haul vary by only 3–14%.

Discussion

Each of the models examined in the previous section—Fox, Schaefer, Schnute, CY&P, and Threshold—appears to estimate valid biological parameters and rea-

Table 5
Static Biological Equilibrium (MSY), Economic Optimum (MEY), and
Economic Equilibrium (OAE) for the Northwestern Hawaiian Islands
Lobster Fishery^a

	Schaefer	Fox	Schnute	CY&P	Threshold
MSY					
<i>Y</i>	877,947	850,015	1,088,219	1,040,393	—
<i>E</i>	722,396	1,039,200	781,595	1,011,195	—
\$	1,849,144	781,144	2,630,060	1,730,540	—
MEY					
<i>Y</i>	814,632	708,127	1,028,422	919,867	1,547,224
<i>E</i>	528,398	530,765	598,379	588,741	997,299
\$	2,137,231	1,645,604	2,902,134	2,436,835	4,077,892
OAE					
<i>Y</i>	689,821	831,376	781,181	960,400	1,889,460
<i>E</i>	1,056,796	1,273,656	1,196,758	1,471,320	2,894,627
\$ ^b	0	0	0	0	0

^a Price equals \$4.55/lobster and cost is \$2.97/trap-haul (Y = number of legal lobsters; E = trap-hauls; \$ = net revenue in 1989 U.S. dollars).

^b By definition, at OAE, profit is equal to zero.

Table 6

Optimal Values for Yield (Y^*), Fishing Effort (E^*), Biomass (X^*), Profit (p), and Catch per Unit Effort (U^*) for the Northwestern Hawaiian Islands Lobster Fishery, with Different Interest Rates (i)

Model	i	Y^*	E^*	X^*	p	U
Schaefer	0	814,632	528,398	3,311,054	2,137,231	1.54
	1	818,570	534,529	3,288,903	2,136,944	1.53
	5	832,408	557,871	3,204,565	2,130,582	1.49
	10	845,995	584,582	3,108,055	2,113,069	1.45
	25	869,350	650,908	2,868,410	2,022,345	1.34
	50	877,893	728,089	2,589,542	1,831,987	1.21
	∞	689,821	1,056,796	1,400,746	0	0.65
Fox	0	708,127	530,765	3,551,329	1,645,604	1.33
	1	713,921	539,760	3,520,723	1,645,254	1.32
	5	734,164	573,236	3,409,116	1,637,934	1.28
	10	754,163	610,135	3,290,190	1,619,338	1.24
	25	792,155	696,224	3,028,611	1,536,521	1.14
	50	821,111	789,271	2,769,223	1,391,921	1.04
	∞	831,376	1,273,656	1,736,031	0	0.65
Schnute	0	1,028,422	598,379	1,882,858	2,902,134	1.72
	1	1,030,604	601,752	1,876,275	2,902,042	1.71
	5	1,038,648	614,779	1,850,854	2,899,955	1.69
	10	1,047,327	630,085	1,820,984	2,893,987	1.66
	25	1,066,209	670,440	1,742,230	2,860,047	1.59
	50	1,082,217	723,551	1,638,582	2,775,143	1.50
	∞	781,181	1,196,758	714,948	0	0.65
CY&P	0	919,867	588,741	1,996,641	2,436,835	1.56
	1	923,231	593,940	1,986,403	2,436,701	1.55
	5	935,542	613,792	1,947,784	2,433,751	1.52
	10	948,707	636,676	1,904,200	2,425,687	1.49
	25	977,505	694,848	1,797,747	2,383,951	1.41
	50	1,004,745	767,141	1,673,708	2,293,179	1.31
	∞	960,400	1,471,320	833,649	0	0.65
Threshold	0	1,547,224	997,299	—	4,077,892	1.55
	1	1,548,737	999,622	—	4,077,877	1.55
	5	1,554,571	1,008,673	—	4,077,539	1.54
	10	1,561,405	1,019,473	—	4,076,559	1.53
	25	1,579,342	1,048,889	—	4,070,806	1.51
	50	1,602,847	1,090,032	—	4,055,558	1.47
	∞	1,889,460	2,894,627	—	0	0.65

sonable economic results for the NWHI lobster fishery. All the models except the Fox model have statistically significant coefficients, but because of the iterative procedure used, the statistical results for the Threshold model have been forced. The Threshold model's estimates contrast markedly with those of the other models. Although this contrast was expected because of the Threshold model's underlying assumptions, we believed it necessary to explore its potential as a viable model for this fishery.

The CY&P model has the best fit with the data ($R^2 = 0.98$) while the Schnute has the strongest t -statistics ($P < 0.02$). The logistic models (Schaefer and Schnute) have a strong body of theoretical literature supporting their applicability to fishery science, whereas models using the Gompertz curve (e.g., the Fox model) apparently have less acceptance.

The choice between the finite difference (Schaefer and Fox) or integrated

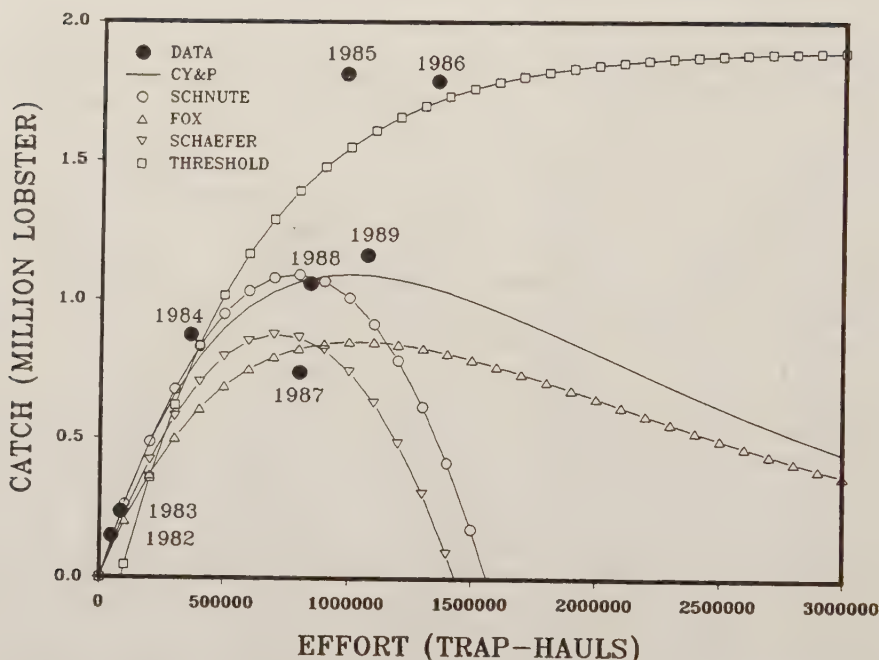


Figure 2. Yield-effort relationships for the Schaefer, Schnute, Fox, CY&P, and Threshold models.

(Schnute and CY&P) models to estimate biological parameters from time series catch and effort data appears to involve a debate over whether the CPUE data employed represent an annual or instantaneous estimate of relative abundance (Pella and Tomlinson, 1969; Schnute, 1977). We believe that the integrated models are theoretically stronger and should be used for the NWHI lobster fishery because of the trends in actual effort and CPUE. For a more complete discussion of dynamic models, see Schnute (1989).

Validation of the CY&P by independent estimates is difficult. Clarke and Pooley (1988) have shown that in aggregate the NWHI commercial lobster fleet broke even during 1986 while expending 1.35 million trap-hauls. If this level of effort is assumed to be approximately representative of OAE, the Fox and CY&P models predict OAE effort accurately. Using similar cost-earnings data and a simple linear CPUE and effort relationship, Samples and Sproul (1987) estimated MEY in the NWHI commercial lobster fishery based on Class II vessels at 893,000 trap-nights with potential economic profits of \$2.33 million. While their estimate of economic profit appears to agree with the values from the CY&P and Schaefer models, predicted effort is different, even when corrected for differences between the effort variables, trap-night versus trap-hauls (cf. Clarke and Todoki, 1988). The MEY predicted by each of our models, with the exception of the Threshold model, falls between 528,000 and 599,000 trap-hauls, substantially less than that predicted by Samples and Sproul (1987). The Fox model is the most conservative and thus deviates the most from their prediction.

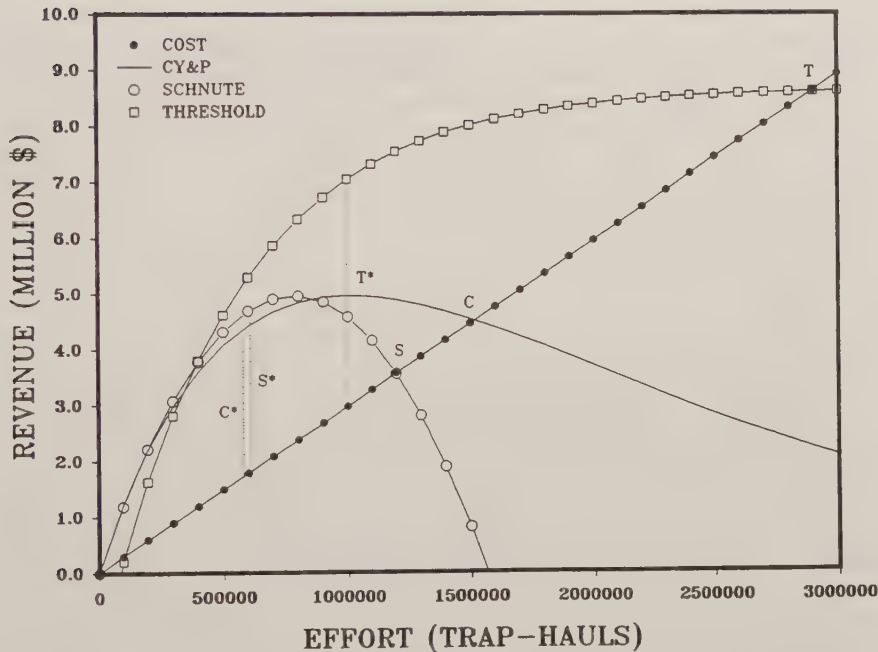


Figure 3. Revenue-effort and cost functions for the Northwestern Hawaiian Islands lobster fishery, using the Schnute (S), CY&P (C), and Threshold (T) models (S, C, and T = the effort levels for open access equilibrium; S^* , C^* , T^* = the net revenue and fishing effort levels for maximum economic yield).

Polovina and Moffitt (1989), using different procedures, estimated MSY for the fishery at 1.14 million spiny and slipper lobsters from 848,000 trap-hauls. The Schnute model best approximates this value in terms of yield (1.1 million), but predicts lower effort levels to obtain the given yield (780,000 trap-hauls). According to Polovina and Moffitt (1989), the yield for 1988 (1.1 million combined spiny and slipper lobsters) falls within the 95% confidence intervals of their model. However, from a bioeconomic point of view, profits (with crews accruing some of the rent) have been estimated at \$1.2 million for the fishery in the same year (Clarke, 1989). This estimate of resource rent (profit) is substantially less than that predicted at MSY effort levels and more in line with that predicted by the CY&P model.

Significant differences in results also are due to the choice of cost estimate (Table 3). These differences are summarized in Table 7. If the CY&P model and the labor opportunity cost adjusted average minimum class II cost (\$2.97 per trap-haul) are used, then fleet profits at MSY are \$1.7 million and resource rent at MEY is \$2.4 million. MEY occurs at 589,000 trap-hauls (919,000 lobsters). With the average minimum class II costs (\$3.52 per trap-haul), without the labor opportunity cost adjustment, profits at MSY drop to \$1.2 million, and MEY is estimated to occur at 536,000 trap-hauls yielding 882,000 lobsters, with potential resource rent of \$2.1 million. Using the fleet average cost per trap-haul (\$4.29),

Table 7

Differences in Resource Rent at Maximum Economic Yield (MEY) and Fleet Profit at Maximum Sustainable Yield (MSY) with Alternative Cost Parameters for the Northwestern Hawaiian Islands Lobster Fishery Using the CY&P Model. Million U.S. Dollars

Cost Alternative ^a	Rent (MEY)	Profit (MSY)
(1) Fleet average	1.7	0.4
(2) Minimum (Class II)	2.1	1.2
(3) Labor opportunity cost (Class II)	2.4	1.7

^a (Table 3)

fleet profits at MSY drop to \$396,000, and MEY effort is 469,000 trap-hauls, yielding 824,977 lobsters and a potential resource rent of \$1.7 million.

The effects of discounting on the models appear to be universally limited for the results presented. All models show that the resource rent will change negligibly even when discounted effort levels may vary as much as 24% over the relevant range. The MEY and associated resource rent are relatively insensitive to choice of discount rates. These results are supported by studies that suggest fisheries management policy is often insensitive to changes in the discount factor over a range of values likely to be found in practice (*e.g.*, Mendelsohn, 1982).

The open access CPUE levels converge to 0.65 for all models as expected, because of the theoretical importance of cost-price ratios in establishing OAE (Clark, 1985). If the minimum fleet average cost per trap-haul (\$2.97) and the 1988 price (\$4.74 per lobster) are used, then CPUE levels at OAE converge at 0.63, which is essentially the same as the ratio of the minimum cost per trap-haul (\$2.97) to the average 1986–1988 ex-vessel price (\$4.55) per lobster. Despite the fact that all major banks had been extensively fished, the OAE CPUE values are substantially below the catch rates exhibited in the fishery over the past 3 years of intensive fishing effort.

Although the CY&P model appears to have a strong fit and validated results, its appropriateness must be tempered. The analysis of the fishery is of one unit stock rather than separating the two major species, spiny and slipper lobster. At the same time, there is noticeable, if not quantifiable, targeting by the fleet as a whole and by segments of the fleet on different species. If a model that integrates the economic and biological differences of the two species were developed, it would more accurately reflect the bioeconomics of the fishery. Presumably size measures could be altered to reflect such differences, or there could be species-specific quotas (either fleet-wide or individual vessel).

Conclusion

With rapidly developing, high-value fisheries such as the NWHI lobster fishery, resource managers have limited research dollars and yet are forced to make management decisions based on relatively limited biological and economic data. Surplus production models are useful in such situations because of their relatively limited data requirements, although some (*e.g.*, Townsend 1986) question their applicability.

All of the models explored show reasonable results, but the CY&P model appears to be the best for economic analysis in the NWHI lobster fishery. This conclusion is tempered by the relatively short time series of data used and the fact that our data set is limited to the ascending limb of the yield-effort relationship. However, Yoshimoto and Clarke (*in press*) applied this model to other lobster catch and effort data and found the CY&P model has an equal or better fit and robustness than the other integrated model explored (Schnute). These fisheries provided substantially longer time series of CPUE data (New Zealand rock lobster, 1945–1987; Tasmanian rock lobster, 1947–1984; American (New England) lobster, 1950–1979).

The use of integrated surplus production models (Schnute and CY&P) as compared to the more conventionally applied Schaefer and Fox finite difference models would allow more liberal effort rates in the NWHI lobster fishery, as well as predicting higher levels of revenue at the economic optima (MEY). However, this may not always be the case and would depend on the catch-effort relationship of the specific fishery for which they are applied. As for the comparison between the integrated models, Schnute (1977) points out that a problem with his model is that the predicted variable, $\bar{U}_{n+1}$, appears on both sides of the regression equation and it is not clear which term should be regressed on ($\ln(\bar{U}_{n+1}/\bar{U}_n)$ or $(\bar{U}_n + \bar{U}_{n+1})/2$). As a result, better regression fits are expected from the CY&P model since its functional form is more straightforward than that of the Schnute model.

Each of the models tested for the NWHI lobster fishery demonstrates that, although the combined yield of spiny and slipper lobsters was not excessive biologically, capital inputs must be adjusted downward if resource rents or profits are to be maximized in the future. The NWHI lobster fishery for 1987–1989 was within MSY norms (given that no data are available on species targeting by fishermen), but by the reference points of the CY&P model, fishing effort has exceeded MEY (assuming "fishing up" has been completed). In the absence of evidence of biological overfishing on the combined stocks and no means of capturing resource rents when restricting effort to MEY levels, there was little likelihood of the adoption of access limitations or individual transferable quotas in order to optimize the fishery economically. Indeed, many participants in the fishery clearly expressed their hostility to effort regulation in 1987–1988 despite the fishery's approach to OAE in 1986. The diminished effort in 1987–1988 suggested that, to a certain extent, the fishery could be self-regulating. Cost-earnings data on vessel operation and performance appeared to confirm our hypothesis that the fishery may be self-regulating. Also supporting this hypothesis are the relatively large investments needed to gear up for fishing and the potentially catastrophic financial results of a shortened or poor trip (Clarke and Pooley 1988).

On the other hand, exogenous events do exist and are as near at hand as the recent, rapid expansion of the Hawaii longline fleet and as distant as the diminishing yields in the Bering Sea, Gulf of Alaska, and Gulf of Mexico fisheries, any of which could bring a large influx of new vessels into the NWHI lobster fishery. The effects of a substantial increase in effort can only be surmised from the models presented. Not surprisingly, faced with the prospect of renewed participation by vessels from Hawaii's other fisheries (*e.g.*, tuna and swordfish longliners), interest in limited entry returned. The limitations of fishery-wide stock production models were also revealed by the apparent recruitment (or catchability) crisis in 1989–90. However, the logistics of regulation and enforcement appear to

mitigate against any bank-by-bank approach to fisheries management. Therefore, assiduous monitoring and evaluation of the key economic and biological signals available in this fishery, including informal information from vessel owners and operators, remain important.

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Appendix A

Derivation of the CY&P Model

Substituting $X = U/q$ into Equation 3 and multiplying both sides by q/U gives

$$(1/U) dU/dt = r \ln(qK) - r \ln(U) - qE.$$

Integrating from $t = \text{year } n$ to $t = \text{year } n + 1$ yields

$$\ln(U_{n+1}/U_n) = r \ln(qK) - r \int_{t=n}^{n+1} \ln(U) dt - q\bar{E}_n; \quad (A1)$$

where U_n is the instantaneous CPUE at the start of year n , and E_n is the total effort for year n .

The first degree Taylor polynomial for $\ln(U)$ centered at $\bar{U}_n$, the average CPUE for year n , is

$$\ln(U) \approx \ln(\bar{U}_n) + (1/\bar{U}_n)(U - \bar{U}_n)$$

$$= \ln(\bar{U}_n) - 1 + (U/\bar{U}_n).$$

Integration of this approximation yields

$$\int_n^{n+1} \ln(U) dt = \ln(\bar{U}_n) - 1 + (1/\bar{U}_n) \int_n^{n+1} U dt. \quad (A2)$$

By definition, $\bar{U}_n = \int_n^{n+1} U dt$, so Equation A2 becomes

$$\int_n^{n+1} \ln(U) dt = \ln(\bar{U}_n) - 1 + 1 = \ln(\bar{U}_n).$$

Putting this result into Equation A1 gives

$$\ln(U_{n+1}/U_n) = r \ln(qK) - r \ln(\bar{U}_n) - q\bar{E}_n.$$

Adding this equation to its corresponding $(n + 1)$ th equation gives

$$\begin{aligned} \ln((U_{n+2}U_{n+1})/(U_{n+1}U_n)) &= 2r \ln(qK) - r(\ln(\bar{U}_n) + \ln(\bar{U}_{n+1})) \\ &\quad - q(\bar{E}_n + \bar{E}_{n+1}). \end{aligned} \quad (A3)$$

We use Schnute's (1977) assumption to estimate for instantaneous CPUE

$$\bar{U}_n = \text{SQRT}(U\langle n + 1 \rangle U\langle n \rangle);$$

that is, the CPUE of a given year is the geometric mean of the CPUE's at the beginning and ending of that year. Plugging this estimate of CPUE into Equation A3 and solving algebraically for $\ln(\bar{U}_{n+1})$ gives

$$\begin{aligned} \ln(\bar{U}_{n+1}) = & (2r/(2 + r)) \ln(qK) + ((2 - r)/(2 + r)) \ln(\bar{U}_n) \\ & - (q/(2 + r))(\bar{E}_n + \bar{E}_{n+1}). \end{aligned}$$

The results of the above equation are dependent on how good an approximation the Taylor polynomial gives. If instantaneous values of CPUE for a given year, n , are suspected to fluctuate considerably away from $\bar{U}_n$, the Taylor approximation becomes invalid and another method to estimate the integral of $\ln(U)$ is needed. As a crude indicator of how reasonable the approximation is, average monthly CPUEs ($\bar{u}_k$ denotes the average monthly CPUE for month k) are assumed to be representative of the instantaneous CPUEs for a given year. The terms $\ln(\bar{u}_k)$ and $(\ln(\bar{U}_n) - 1 + \bar{u}_k/\bar{U}_n)$ are summed for a given year, n , divided by 12, and compared:

Year	$\left(\sum_{k=1}^{12} \ln(\bar{u}_k) \right) / 12$	$\left(\sum_{k=1}^{12} A_k \right) / 12$	% Error
1983	1.08	1.13	+ 4.60
1984	1.27	1.30	+ 1.90
1985	0.93	0.95	+ 2.19
1986	0.62	0.64	+ 2.26
1987	0.27	0.31	+ 14.95
1988	0.50	0.55	+ 9.52

Note: $A_k = \ln(\bar{U}_n) - 1 + \bar{u}_k/\bar{U}_n$.

The Taylor approximation appears to introduce relatively small errors, and its use with the above data appears warranted.

Appendix B

Derivation of Discounting for the Threshold Model

From the Threshold model, with catch written as G

$$\begin{aligned} \ln(A - G) &= \ln(B) - kE \\ &= \ln(B) - kG/(qX). \end{aligned}$$

Taking the derivative (with respect to X) of both sides:

$$(-1/(A - G))G'[X] = -k/q((1/X)G'[X] - G/X^2).$$

Solving for $G'[X]$

$$G'[X] = \frac{kG/(qX^2)}{k/(qX) - 1/(A - G)}.$$

Inserting $G'[X]$ and $c'[X] = -c/(qX^2)$ into Equation 12 yields

$$\frac{kG/(q(X^*)^2)}{k/(qX^*) - 1/(A - G)} + \frac{cG/(q(X^*)^2)}{p - c/(qX^*)} = \delta.$$

Multiplying both sides by $q(X^*)^2/G$ yields

$$\frac{k}{k/(qX^*) - 1/(A - G)} + \frac{c}{p - c/(qX^*)} = \frac{\delta q(X^*)^2}{G}.$$

Plugging in $G/(qE^*)$ for X^* gives Equation 18 in the text.

Differences in Dolphin Mortality Rates in Night and Day Sets for the U.S. Eastern Tropical Pacific Tuna Purse Seine Fishery

ATILIO L. COAN, Jr., KENNETH E. WALLACE, and ALAN R. JACKSON

Introduction

The association of yellowfin tuna, *Thunnus albacares*, with dolphins (mainly *Stenella attenuata* and *S. longirostris*) in the eastern tropical Pacific (ETP) (Fig. 1) has been used by purse seine fishermen to harvest yellowfin tuna since the early 1960's (McNeely, 1961). Purse seiners locate dolphin pods and use speed boats to herd the dolphins into purse seine nets to capture the tuna traveling below them (dolphin sets). As the dolphins are surrounded by the purse seines, some may become entangled and drown before they can be released alive (Perrin, 1969; Green et al., 1971).

While all dolphin sets start in daylight, they sometimes extend into dark-

ness. When this occurs, more animals are killed because the release of entangled dolphins is complicated by the inability to see the animals (IATTC, 1984). Sets can also last longer (sometimes into darkness) if equipment malfunctions, strong currents, high winds, net collapses (cork lines come together, Coe et al., 1984), or canopies (net blossoms out beyond the cork line, Coe et al., 1984) occur. These problems subject dolphins to longer periods of time in the nets and contribute to higher dolphin mortality. Estimated annual dolphin mortality for the ETP international purse seine fleet was as high as 550,000 animals in 1961 (Smith, 1983) and public concern over the numbers of dolphins killed prompted the U.S. Government and U.S. industry to take steps to monitor and reduce this mortality (Fox, 1978).

Monitoring of the incidental dolphin mortality began in 1971 when the National Marine Fisheries Service (NMFS) placed scientific technicians (observers) on U.S. purse seiners fishing in the ETP. In 1979, the Inter-American Tropical Tuna Commission (IATTC) started its own international tuna-dolphin program that placed observers on both U.S. and foreign purse seiners. U.S. regulations were enacted to reduce ETP dolphin mortality through the Marine Mammal Protection Act (MMPA) in 1972, and various reauthorizations of the Act led to the establishment of the current mortality quota of 20,500 dolphins for the U.S. fleet.

Reductions in dolphin mortality were accomplished by modifying purse

seines and purse seining operations (Coe et al., 1984). The "Medina panel," a portion of the purse seine net with 1-inch mesh, was developed to reduce dolphin entanglement, and backdown procedures, methods used to submerge a portion of the net, were developed to aid in the release of dolphins (Barham et al., 1977; Coe and Sousa, 1972). In the early 1980's, the U.S. tuna industry also experimented with high-intensity 140,000-lumen floodlights. These high-intensity floodlights were used to reduce dolphin mortality in dolphin sets made at night by making dolphins in the net more visible and aiding the release of captured animals. The high-intensity floodlights became a mandatory requirement for all certificated (licensed to fish on dolphins) U.S. vessels on 1 July 1986.

Our study uses data collected through the NMFS and IATTC monitoring programs, during 1979-88, to look at differences between mortality rates in day and night sets made by U.S. purse seiners fishing in the ETP. The benefits of using high-intensity floodlights to decrease night set mortality rates are assessed, a regulation aimed at eliminating night sets is simulated, and the benefits to mortality rates quantified.

Data and Methods

Data from over 20,000 dolphin sets that produced approximately 302,000 short tons (tons) of yellowfin tuna were collected by IATTC and NMFS observers on U.S. purse seiners fishing in the ETP during the period 1 January 1979 to 31 December 1988. Many types of

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ABSTRACT—Because dolphins sometimes travel with yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific (ETP), purse seiners use the dolphins to locate and capture tuna schools. During the process of setting the purse seine nets, dolphins often become entangled and drown before they can be released. Data for the U.S. purse seine fleet in the ETP during 1979-88 show that dolphin mortality rates in sets made during the night are higher than mortality rates in sets made during the day. Even with efforts to reduce night-set mortality rates through the use of high-intensity floodlights, night set mortality rates remain higher. The data are also used to simulate a regulation on the fishery aimed at eliminating night sets and show that dolphin mortality rates would decrease.

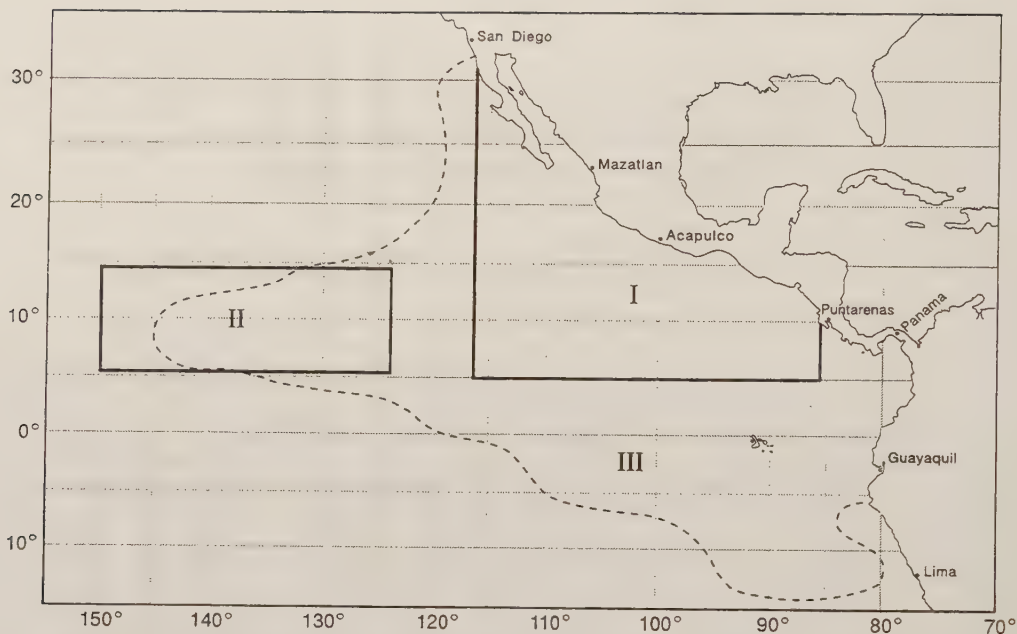


Figure 1.—Area of the eastern tropical Pacific (ETP) historically fished for yellowfin tuna associated with dolphins (dotted line) and three subareas of the ETP used to stratify data in this study and define regions of differing dolphin mortality rates. Area I is the northern coastal inshore area, area II, the offshore area, and area III is all other ETP areas.

data were collected by these observers; however, only information concerning times of various events in the set (e.g., sundown, backdown, etc.), numbers of dolphins killed, geographical location, tons of yellowfin tuna caught, and night light use for each set, was used in this analysis.

Data were divided into night sets (sets started during daylight or twilight hours but with any portion of the backdown occurring in darkness) and day sets (sets started during daylight hours and backdown procedures completed in daylight or twilight hours). For sets where no backdown information was recorded, the time of the end of the set was compared to the time of sunset, and those sets that ended before sunset were considered day sets. Those that ended after sunset were eliminated. If the time of sundown was not recorded, sundown times were calculated from the geographical position and date (Bowditch, 1966). Calculated sundown times are

accurate to ± 3 minutes for positions between lat. 30°N and 30°S .

In the process of separating day and night sets and computing dolphin mortality rates, certain sets were eliminated: 1) All sets where marine mammals were accidentally caught (e.g., sets on floating objects or free swimming schools of tuna where dolphins were not intentionally herded into nets); 2) sets where the tons of yellowfin caught or the numbers of marine mammals killed were not recorded; or 3) dolphin sets where there was no backdown information and the set terminated after sunset. Approximately 2% of the dolphin sets, 1% of the total dolphin mortality, and 1% of the total yellowfin tuna catch were eliminated by deleting sets that met any of these criteria.

Ninety percent (18,873) of the observed ETP dolphin sets during 1979–88 were day sets that accounted for 90% of the yellowfin tuna catch (270,916 tons) and 70% of the dolphin mortality

(58,341). Night sets were much less frequent, with 10% of the dolphin sets (1,849), 10% of the yellowfin tuna catch (29,406 tons) and 30% of the dolphin mortality (25,261). The number of night sets for the entire ETP ranged from 74 to 402 and day sets from 762 to 3,891 annually (Table 1). The number of dolphins killed for the entire ETP ranged from 399 to 4,468 in night sets and 2,573 to 10,533 in day sets.

Data for night and day sets were stratified into three subareas of the ETP to assess the effects of geographical location on differences between mortality rates in day and night sets (Fig. 1). The three subareas chosen encompass regions of the ETP having significant differences in mortality rates and are standard subareas used in development of ETP dolphin fishing regulations (Federal Register, 1988, 1989). Area I contains a major portion of the northern coastal region of the ETP that is historically fished for yellowfin tuna

Table 1.—Number of sets and dolphin mortality (animals killed) for day and night sets of U.S. purse seiners fishing in the entire eastern tropical Pacific (ETP) and three subareas.

Year	Entire ETP		Area I		Area II		Area III	
	Day	Night	Day	Night	Day	Night	Day	Night
Number of sets								
1979	2,658	248	1,890	172	351	23	387	51
1980	2,023	159	1,308	103	377	30	336	26
1981	2,065	172	1,305	108	466	35	291	29
1982	1,686	206	1,011	114	217	37	451	55
1983	905	74	361	22	287	23	252	28
1984	762	104	408	51	195	32	158	21
1985	1,787	197	1,476	161	179	23	132	13
1986	1,295	162	871	90	411	47	209	25
1987	3,891	402	3,004	279	387	64	495	59
1988	1,801	168	1,197	123	137	4	467	41
Dolphin mortality								
1979	5,289	2,432	2,770	1,480	1,024	120	1,455	809
1980	4,720	1,911	1,872	427	1,198	210	1,635	1,274
1981	5,724	2,004	2,532	654	1,326	536	1,866	814
1982	6,692	2,695	2,733	1,210	493	697	3,429	788
1983	2,573	399	525	83	1,125	47	923	265
1984	2,673	2,444	1,100	1,432	662	693	911	319
1985	6,225	3,047	4,580	2,115	870	668	775	264
1986	5,781	4,468	2,263	2,106	1,512	2,042	2,001	320
1987	10,533	3,519	6,344	1,996	1,142	679	3,047	844
1988	8,131	2,342	3,978	615	1,136	10	3,017	1,717

associated with dolphins. Area II contains the offshore region, and area III contains all other regions of the ETP not contained in areas I or II.

Sixty-seven percent of the observed ETP dolphin sets during 1979-88 occurred in area I, 16% in area II, and 17% in area III (Table 1). Forty-nine percent of the dolphin mortality occurred in area I, 19% in area II, and 32% in area III. The average number of observed night and day sets (32 and 301) and dolphin mortality (570 and 1,049) was lowest in area II.

Dolphin night sets were divided into sets using high-intensity floodlights and sets using other types of lights (e.g., low-intensity lights). Data for 722 night sets that used high-intensity floodlights were available for 1982-88 only and ranged from a low of 9 in 1983 to a high of 327 in 1987. Data for 451 night sets that used other types of light were available for 1982-88 and ranged from a low of 21 in 1988 to a high of 146 in 1982. In 1982-86, high-intensity floodlights were loaned to only a select group of vessels to test their usefulness. After 1986 the lights were available to all vessels. Due to the limited number of sets that used high-intensity floodlights or other types of

light, comparisons of mortality rates for these sets were not stratified by subareas of the ETP.

Two mortality rates were calculated: The total number of dolphins killed divided by the total number of dolphin sets (kill/set); and total number of dolphins killed divided by the total tonnage of yellowfin tuna caught (kill/ton) in dolphin sets. Percentages of dolphin sets with zero dolphins killed (zero-kill sets) and percentages of dolphin sets with more than 15 dolphins killed (high-kill sets) were also calculated.

The Wilcoxon paired-sample test (Zar, 1974; Siegel, 1956) was used to determine significant differences (at the 5% level) between the following pairs of data: 1) Mortality rates in day sets vs. night sets, 2) percentages of high-kill sets in day sets vs. night sets, 3) percentages of zero-kill sets in day sets vs. night sets, and 4) mortality rates in sets that used high-intensity floodlights vs. sets that used other types of light. The pairs of data considered were yearly estimates. The test considers the magnitude and occurrences of positive and negative differences between the estimates in determining whether the differences are randomly distributed. The null hypothesis was that the esti-

mated mortality rates, percentages of zero-kill sets, and percentages of high-kill sets were the same in day and night sets, or that the mortality rates in night sets that used high-intensity floodlights and those that used other types of lights were the same. A nonparametric statistical test was chosen because estimated mortality rates were not normally distributed. The distributions were basically Poisson with the major mode occurring at zero dolphins killed (Fig. 2).

Linear regressions were used to define trends in yearly estimates of mortalities and mortality rates. These trends were considered significant (5% level) if the regression coefficients were statistically different from zero. The Student's T statistic was used to determine significance. To guarantee that the regression coefficients were of minimum variance, autocorrelation was assessed with a Runs test and Durbin-Watson statistic on the residuals (Smillie, 1966).

Results

The number of observed sets and dolphin mortality in most areas of the ETP was highest in 1987, when observer coverage was 92% and lowest in 1983 (31% observer coverage) or 1984 (28% observer coverage), when a court injunction limited the placement of observers. While this relationship of higher estimates in high coverage years and lower estimates in low coverage years may imply an autocorrelation between coverage rates and mortality and mortality rate estimates, no positive or negative autocorrelation was detected at the 5% level of significance. Therefore, esti-

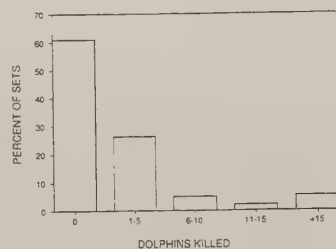


Figure 2.—A typical distribution of mortality rates in dolphin sets of U.S. purse seiners fishing in the eastern tropical Pacific.

Table 2.—Statistical comparisons of mortality rates and percentages of zero-kill and high-kill (more than 15 dolphins killed) sets in the entire eastern tropical Pacific and three subareas. Values of the Wilcoxon's T statistic greater than eight are considered significant at the 5% level, except for high-intensity light comparisons that are significant if values are greater than three.

Comparison	Wilcoxon's T statistic	Conclusion
Kill/set day vs. night		
Entire ETP	0	Night sets higher
Area I	0	Night sets higher
Area II	5	Night sets higher
Area III	0	Night sets higher
Kill/ton day vs. night		
Entire ETP	0	Night sets higher
Area I	0	Night sets higher
Area II	5	Night sets higher
Area III	0	Night sets higher
% Zero-kill sets day vs. night		
Entire ETP	0	Night sets lower
Area I	0	Night sets lower
Area II	0	Night sets lower
Area III	3	Night sets lower
% High-kill sets day vs. night		
Entire ETP	0	Night sets higher
Area I	0	Night sets higher
Area II	4	Night sets higher
Area III	1	Night sets higher
High-intensity lights vs. other lights		
Kill/set entire ETP	0	Other light higher
Kill/ton entire ETP	1	Other light higher
High-intensity lights vs. day sets		
Kill/set entire ETP	0	High-intensity light higher
Kill/ton entire ETP	1	High-intensity light higher
Kill/set Area I vs. Area II		
Day sets	2	Area II higher
Night sets	13	No significant difference
Kill/set Area I vs. Area III		
Day sets	0	Area III higher
Night sets	13	No significant difference
Kill/set Area II vs. Area III		
Day sets	6	Area III higher
Night sets	18	No significant difference
Kill/ton Area I vs. Area II		
Day sets	13	No significant difference
Night sets	26	No significant difference
Kill/ton Area I vs. Area III		
Day sets	0	Area III higher
Night sets	15.5	No significant difference
Kill/ton Area II vs. Area III		
Day sets	4.5	Area III higher
Night sets	15	No significant difference
Zero-kill Area I vs. Area II		
Day sets	0	Area I higher
Night sets	0	Area I higher
Zero-kill Area I vs. Area III		
Day sets	6	Area I higher
Night sets	0	Area I higher
Zero-kill Area II vs. Area III		
Day sets	1	Area II higher
Night sets	19	No significant difference
High-kill Area I vs. Area II		
Day sets	6	Area I lower
Night sets	15	No significant difference
High-kill Area I vs. Area III		
Day sets	0	Area I lower
Night sets	4	Area I lower
High-kill Area II vs. Area III		
Day sets	1	Area II lower
Night sets	12	No significant difference

mates of mortality rates and mortalities are randomly ordered and independent of yearly coverage rates, and trends generated from simple regressions will properly estimate the variance.

ETP night set dolphin mortality rates (kill/set and kill/ton) were significantly higher than ETP day set mortality rates during 1979-88 (Table 2). Day set kill/set ranged from 1.99 to 4.51 dolphins per set and for night sets from 0.5 to 27.58 dolphins per set (Fig. 3). Day set kill/ton ranged from 0.19 to 0.38 dolphins/ton and for night sets from 0.5 to 1.31 dolphins/ton. A significant increasing trend during 1979-88, was detected in kill/set for day sets (Table 3).

Night set mortality rates were significantly higher in all three subareas of the ETP than day set mortality rates (Table 2). Dolphin mortality rates in day sets were generally lower in area I than in areas II and III, whereas no significant differences in night set mortality rates between areas were detected. Mortality rates were highest in area III in 1980 when kill/set was 49 dolphins/set and kill/ton was 4.39 dolphins/ton. Night set mortality rates were always higher than day set mortality rates, except in area II in 1983 and 1988 (Fig. 3). Significant increasing trends during 1979-

Table 3.—Kill/set and kill/ton for day and night sets in the entire eastern tropical Pacific (ETP) and three subareas. The Student's T statistic is used to detect significant trends in the data. Values greater than ± 2.306 are significant at the 5% level. Positive values indicate increasing trends and negative values reflect decreasing trends.

Year	Entire ETP		Area I		Area II		Area III	
	Day	Night	Day	Night	Day	Night	Day	Night
Kill/set								
1979	1.99	9.81	1.46	8.60	2.92	5.22	3.76	15.86
1980	2.33	12.02	1.43	4.14	3.18	7.00	4.87	49.00
1981	2.77	11.65	1.94	6.06	2.84	15.31	6.41	28.07
1982	3.97	13.08	2.70	10.61	2.27	18.84	7.60	14.32
1983	2.84	5.39	1.45	3.77	3.92	2.04	3.66	9.46
1984	3.51	23.50	2.70	28.08	3.39	21.66	5.76	15.19
1985	3.48	15.47	3.10	13.14	4.86	29.04	5.87	20.31
1986	4.46	27.58	3.37	23.40	3.68	43.45	9.57	12.80
1987	2.71	8.75	2.11	7.15	2.95	10.61	6.16	14.30
1988	4.51	13.94	3.32	5.00	8.29	2.50	6.46	41.88
Student's T	2.74	0.97	3.04	0.68	2.24	0.78	1.56	-0.24
Kill/ton								
1979	0.20	0.79	0.16	0.83	0.25	0.47	0.26	0.87
1980	0.23	1.09	0.18	0.43	0.22	0.45	0.37	4.39
1981	0.26	1.02	0.21	0.63	0.22	0.93	0.48	2.25
1982	0.38	0.98	0.31	1.03	0.19	1.17	0.55	0.80
1983	0.28	0.50	0.22	0.55	0.30	0.18	0.29	0.68
1984	0.18	0.31	0.15	1.82	0.17	1.07	0.28	0.75
1985	0.20	0.81	0.18	0.71	0.20	1.24	0.44	1.12
1986	0.15	1.03	0.17	0.92	0.12	1.39	0.41	0.55
1987	0.26	0.50	0.13	0.45	0.13	0.54	0.31	0.68
1988	0.19	0.76	0.20	0.29	0.44	0.17	0.34	1.95
Student's T	-0.88	-0.85	-0.69	-0.35	0.27	0.15	-0.21	-1.11

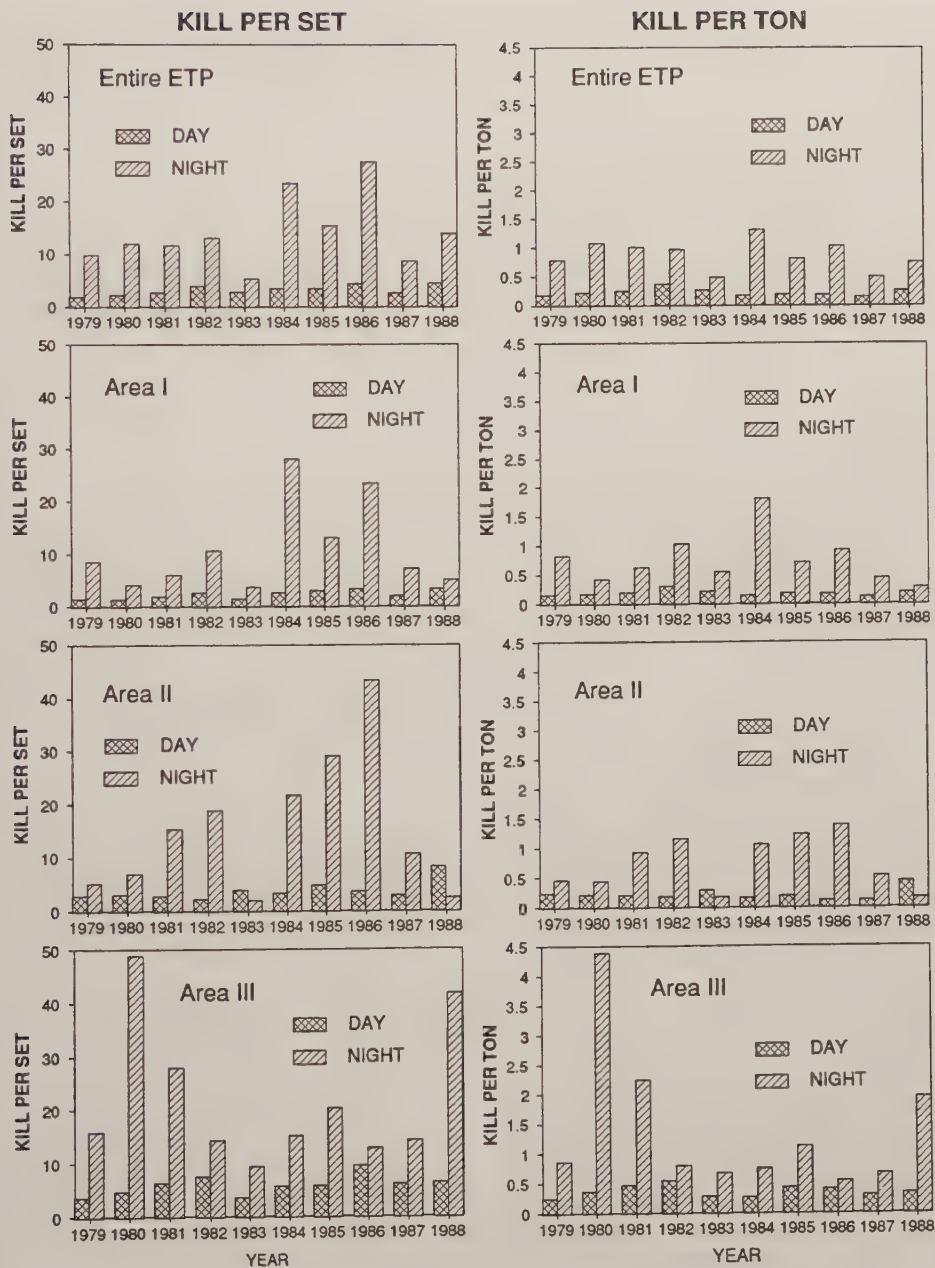


Figure 3.—Kill/set and kill/ton in day and night sets of U.S. purse seiners fishing in the eastern tropical Pacific (ETP) and three subareas of the ETP.

88 were detected in kill/set for day sets in area I only (Table 3).

Day sets in the ETP had significantly

higher percentages of zero-kill sets and lower percentages of high-kill sets than night sets (Table 2). Night set zero-kill

percentages ranged from 36 to 51%, whereas day set percentages ranged from 52 to 71% (Figure 4). Percent-

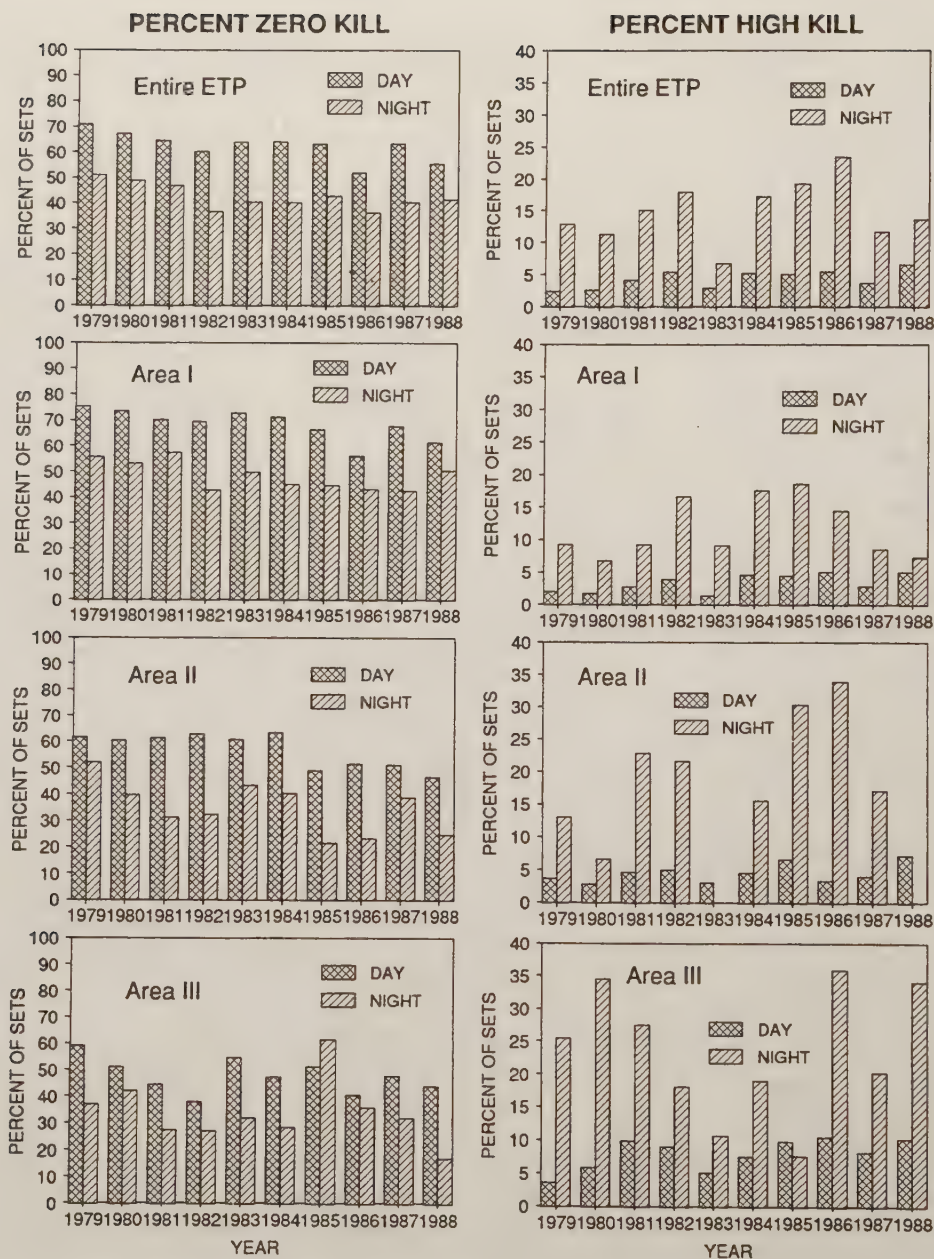


Figure 4.—Percentages of zero-kill sets and high-kill sets in day and night sets of U.S. purse seiners fishing in the eastern tropical Pacific (ETP) and three subareas of the ETP.

ages of high-kill sets ranged from 7 to 23% for night sets and 2 to 7% for day sets. The greatest differences between the percentages occurred in zero-kill

sets, where day sets were as much as 20% higher than night sets. Significant decreasing trends in both day and night set percentages of zero-kill sets during

1979-88, were detected (Table 4).

Stratified percentages of zero-kill sets in night sets were significantly lower than in day sets for all subareas

Table 4.—Percentages of zero-kill sets and high-kill sets (more than 15 dolphins killed) for day and night sets in the entire eastern tropical Pacific (ETP) and three subareas. The Student's T statistic detects significant trends in the data. Values greater than ± 2.306 are significant at the 5% level. Positive values indicate increasing trends and negative values reflect decreasing trends.

Year	Entire ETP		Area I		Area II		Area III	
	Day	Night	Day	Night	Day	Night	Day	Night
Zero-kill								
1979	71.07	51.21	75.34	55.81	61.82	52.17	59.43	37.25
1980	67.47	49.06	73.70	53.40	60.74	40.00	51.19	42.31
1981	64.75	47.09	70.29	57.41	61.59	31.43	44.67	27.59
1982	60.26	36.89	69.44	42.98	63.13	32.43	38.14	27.27
1983	64.20	40.54	72.85	50.00	60.98	43.48	54.76	32.14
1984	64.44	40.38	71.32	45.10	63.59	40.62	47.47	28.57
1985	63.51	43.15	66.33	44.72	49.16	21.74	51.52	61.54
1986	52.12	36.42	56.18	43.33	51.58	23.40	40.67	36.00
1987	63.61	40.55	67.74	42.65	51.16	39.06	47.88	32.20
1988	55.91	41.67	61.57	50.41	46.72	25.00	44.11	17.07
Student's T	-3.01	-2.53	-3.44	-2.34	-4.04	-2.17	-1.31	-0.50
High-kill								
1979	2.41	12.90	1.96	9.30	3.70	13.04	3.62	25.49
1980	2.62	11.32	1.68	6.80	2.92	6.67	5.95	34.62
1981	4.21	15.12	2.76	9.26	4.72	22.86	9.97	27.59
1982	5.46	17.96	3.86	16.67	5.07	21.62	9.09	18.18
1983	2.98	6.76	1.39	9.09	3.14	0.00	5.16	10.71
1984	5.25	17.31	4.66	17.65	4.62	15.62	7.59	19.05
1985	5.09	19.29	4.47	18.63	6.70	30.43	9.85	7.69
1986	5.41	23.46	5.07	14.44	3.41	34.04	10.53	36.00
1987	3.68	11.69	2.86	8.60	4.13	17.19	8.28	20.34
1988	6.61	13.69	5.10	7.32	7.30	0.00	10.28	34.15
Student's T	-0.88	-0.85	-0.69	-0.35	0.27	0.15	-0.21	-1.11

of the ETP, and percentages of high-kill sets in night sets were significantly higher than in day sets (Table 2). Percentages of zero-kill sets were significantly lower for both day and night sets in areas II and III than in area I. However, areas II and III generally had significantly higher percentages of high-kill sets than area I. Percentages of zero-kill sets were always lower in night sets than in day sets except for area III in 1985 (Fig. 4). Percentages of high-kill sets were always higher in night sets than in day sets, except in 1983 and 1988 in area II, and 1985 in area III. Significant decreasing trends were found in the percentages of zero-kill sets for day sets in areas I and II and for night sets in area I (Table 4).

Comparisons of Floodlight Use in Night Sets

During 1982-88, night sets using high-intensity floodlights generally produced significantly lower mortality rates (4-77%) than night sets using other types of lights (Table 2). Only in 1985 did kill/ton for night sets that used other lights fall below kill/ton in night sets that used high-intensity floodlights (Fig. 5). The greatest difference oc-

curred in 1984 when kill/set in sets using high-intensity floodlights was approximately 77% lower than kill/set in sets using other types of light. High-intensity floodlights were therefore effective in reducing night set mortality rates. However, mortality rates were

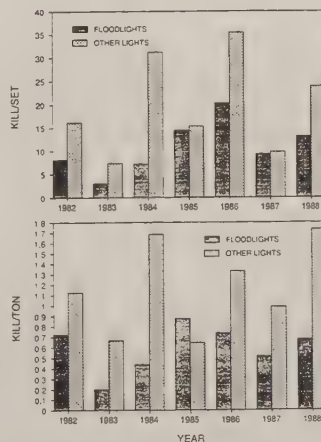


Figure 5.—Kill/set and kill/ton in night sets of U.S. purse seiners fishing in the eastern tropical Pacific that used high-intensity floodlights or other types of lights.

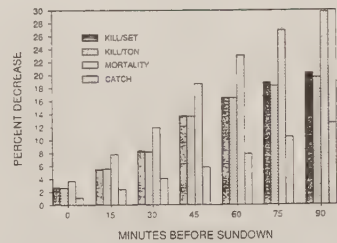


Figure 6.—Percent decreases in kill/set, kill/ton, dolphin mortality, and yellowfin catch if sets beginning after sundown or at various times before sundown (e.g., 15, 30, 45, etc., minutes) were eliminated from dolphin sets made by U.S. purse seiners fishing in the eastern tropical Pacific during the period 1979 to 1988.

still significantly lower in day sets (Table 2).

Effects of Prohibiting Night Sets

Night sets begin before sundown or during the twilight hours, while herds of dolphins can still be seen, extend into darkness, and are usually completed before midnight. Regulations prohibiting these night sets were simulated by selecting time limits (sundown and 15, 30, 45, 60, 75, and 90 minutes before sundown), eliminating both day and night sets starting after each of these time limits and calculating and comparing the new total (day and night sets combined) mortality rates to rates before any sets were eliminated.

Results showed that average total mortality rates for 1979-88, decreased approximately 6-20% (Fig. 6), depending on the time limit chosen. Total mortality decreased as much as 30% and catches dropped 13%.

The simulation did not eliminate all night sets. Even by prohibiting sets starting after 90-minutes before sun-

down, 144 night sets that killed 3,651 animals still remained. Some of these sets started as much as 5 hours before sundown and, because of problems during the set or other reasons, extended into darkness. The resulting average kill/set of 25 dolphins per set for these sets was almost 79% higher than the average kill/set in the ETP (14 dolphins/set) before any night sets were eliminated.

The simulation also eliminated valid day sets that started after the time limits and, because operations went so quickly, were completed before darkness. Under the 90-minute set prohibition, 705 sets or approximately 4% of the valid day sets were lost along with 4% (9,800 tons) of the yellowfin tuna catch.

Discussion

Our results show that night sets, while contributing only 30% of the observed mortality, killed animals at a significantly higher rate than day sets. Stratification of the data by the three subareas did not change these results.

Factors such as proximity of the start of the set to sundown, size of the yellowfin catch, and problems that occur during dolphin sets extend sets into darkness where higher mortalities occur. Fishermen have tried to reduce the effects of darkness in night sets through the use of high-intensity floodlights. While these lights decreased mortality rates in night sets by making animals in the net more visible, mortality rates in sets using these lights were still significantly higher than day set mortality

rates, probably because animals that are usually seen in daylight, i.e., just below the surface and at the fringes of the lighted area, still go undetected.

It appears that all past efforts to eliminate the significant differences between day and night set mortality rates failed, probably due to the unique factor that darkness plays in making dolphins more vulnerable during night sets. However, our study shows that through regulations aimed at reducing the number of night sets while minimizing the effect on day sets, substantial decreases in overall mortality rates (day and night sets combined) can be attained. Since some night sets would still occur under these regulations, additional decreases in mortality rates could be made if they were eliminated.

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PHYLOGENY AND ECOLOGY OF A KELP-BORING AMPHIPOD,
PERAMPHITHOE STYPTOTRUPETES, NEW SPECIES
 (COROPHIOIDEA: AMPITHOIDAE)

K. E. Conlan and J. R. Chess

ABSTRACT

A new species of amphithoid amphipod has been found which bores into and occupies the interior of abraded stipes of kelps on the Pacific coast of North America. Adult bisexual pairs cohabit the stipes with their offspring of several generations. *Peramphithoe stypotrumpetes*, new species, is diagnosed, illustrated, and its boring habits are described. The type for the genus, *Peramphithoe femorata* (Krøyer, 1845), is redescribed and illustrated, and compared with the new species. *Peramphithoe stypotrumpetes* can be distinguished from *P. femorata* and other eastern Pacific species of the genus by its shorter pair of first antennae and narrower pereopod 3 and 4 bases. Relationships are compared cladistically and biogeographically, and presented in a key.

A new species of amphithoid amphipod, *Peramphithoe stypotrumpetes*, has been discovered by one of us (JRC) inhabiting the stipes of laminarian phaeophytes on the exposed coasts of California and southeastern Alaska. This is the first record of kelp-boring for this genus and the second record for the family Amphithoidae. The purpose of this paper is to describe this new species, to compare it with the type for the genus, *Peramphithoe femorata* (Krøyer, 1845), and other eastern Pacific members of the genus, and to set a hypothesis for its phylogeny and biogeography.

MATERIALS AND METHODS

Type specimens were illustrated, using a camera lucida, from the undissected body stained with methylene blue, and from individual appendages mounted in polyvinyl lactophenol and stained with lignin pink. Body lengths were measured by eyepiece micrometer, from the tip of the rostrum to the base of the telson. The diagnoses encompass characters that distinguish *Peramphithoe stypotrumpetes* from other eastern Pacific species of the genus described in Conlan and Bousfield (1982). Cladistic analyses were conducted on all species of *Peramphithoe* occurring in the eastern Pacific (*P. tea* (Barnard, 1965), *P. plea* (Barnard, 1965), *P. lindbergi* (Gurjanova, 1938), *P. mea* (Gurjanova, 1938), *P. humeralis* (Stimpson, 1864), *P. femorata* (Krøyer, 1845), *P. stypotrumpetes*, new species, and *P. lessoniophila* Conlan and Bousfield, 1982). The outgroup species was *Ampithoe lacertosa* Bate, 1858. All external characters that exhibited discontinuities within the species-group were selected for analysis. Quantitative characters were regressed against characters that were isometric with body size. Scores for the quantitative characters were

derived from the residuals by plotting each value and assigning a score to each cluster of residuals. The cluster containing the outgroup residual was assigned a score of zero in all cases. Cladistic analyses were run on the programs Hennig86 and PAUP version 2.4. Since the data set was small, the ie option was invoked for Hennig86 and the ALLTREES option for PAUP, in order to ensure trees of minimal length. Nelson consensus trees were computed for multiple trees generated by each program.

RESULTS

Species Descriptions

Peramphithoe stypotrumpetes,
 new species
 Figs. 1-3

Adult Female.—Holotype: Length 19.6 mm. Body moderately stout, head dorsally bulbous. Eye moderately large. Antenna 1, peduncle overlapping only first 25% of antenna 2 peduncular article 4; peduncle article 1 without spine at posterodistal corner; article 2 75% of length of article 1. Antenna 2, flagellum moderately setose, proximal articles fused. Mandible, lacinia mobilis with 5 teeth left, 7 teeth right, raker spines 10 left, 10 right; palp article 3 with setae on distal and distoventral margins. Maxilliped, palp article 4, width 52% of article 3 width. Gnathopods 1 and 2 and pereopods 3 and 4, bases densely setose posteriorly and medially. Gnathopod 1, carpus 94% of propodus length; dactyl extending beyond palm of propodus by 40% of its length. Gnathopod 2, propodus maximally 160% of width of propodus of gnathopod 1; palm shallowly concave. Pereiopod 3, basis 152% of width of basis of gnathopod 2, width 52% of length;

Dedicated to Dr. J. L. Barnard of the Smithsonian Institution, who died 16 August 1991.

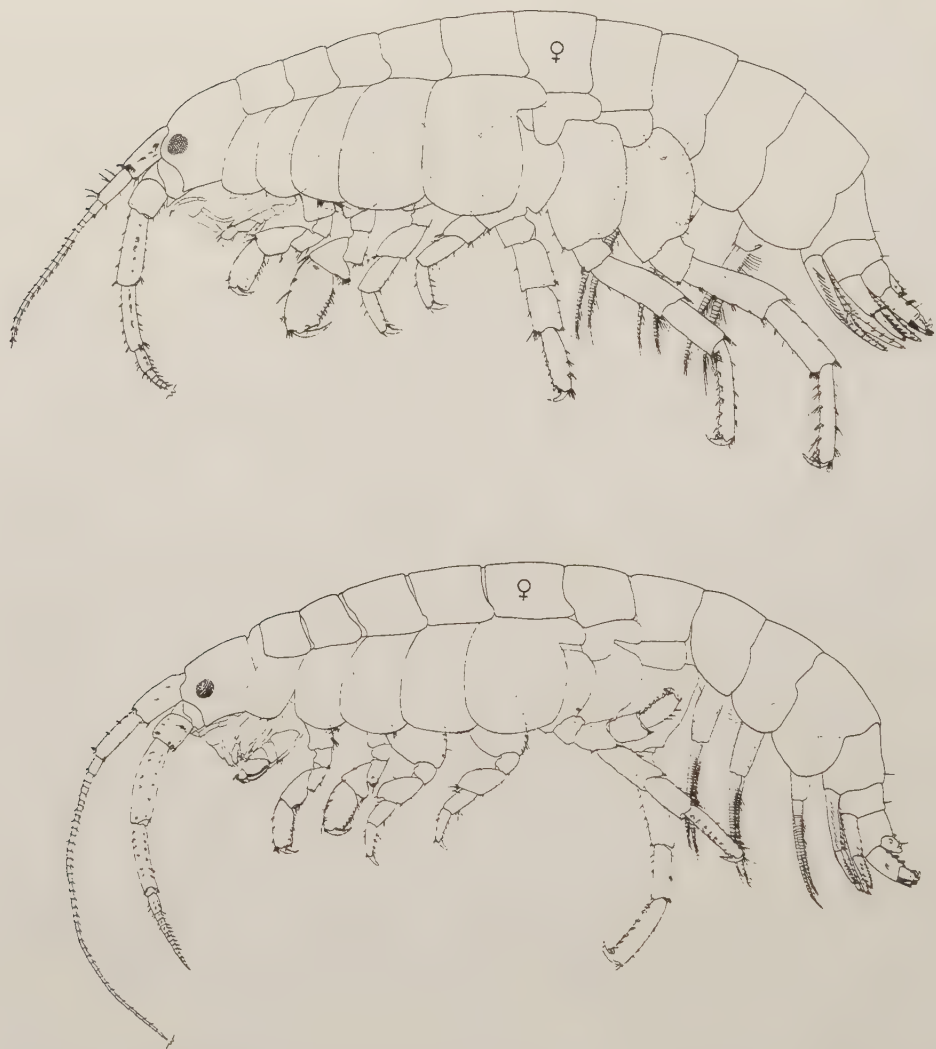


Fig. 1. Above: *Peramphithoe stypotrumpetes*, new species. Holotype, female, 19.6 mm, Whitesboro Cove, Mendocino County, California, 28 February 1985, J. R. Chess, collector. The first antenna is taken from a paratype, female, 16.1 mm, Bird Rock, Santa Catalina Island, Los Angeles County, California, 13 May 1980. Below: *Peramphithoe femorata* (Krøyer). Lectotype, female, 20.8 mm, Valparaíso, Chile.

merus, width 150% of width of carpus. Pereiopod 5, basis, width 118% of length. Pereiopod 7, length 103% of pereopod 6; bases posteriorly convex; propodus with 8 spine groups. Uropods 1 and 2, rami slender and densely spinose. Uropod 3, peduncle more than twice length of rami.

Condition.—Brooding hatchlings. Both antennae 1 and 2 lack flagellar tips. Right ap-

pendages, telson, and mouthparts slide-mounted; other appendages with carcass.

Adult Male.—Allotype: Length 13.1 mm. Gnathopod 2, propodus, palm with shallow tubercle proximal to dactyl insertion and indentation proximal to tubercle; dactyl extending through half length of propodus, palmar defining spine absent.

Condition.—Missing right pereopods 3, 5,

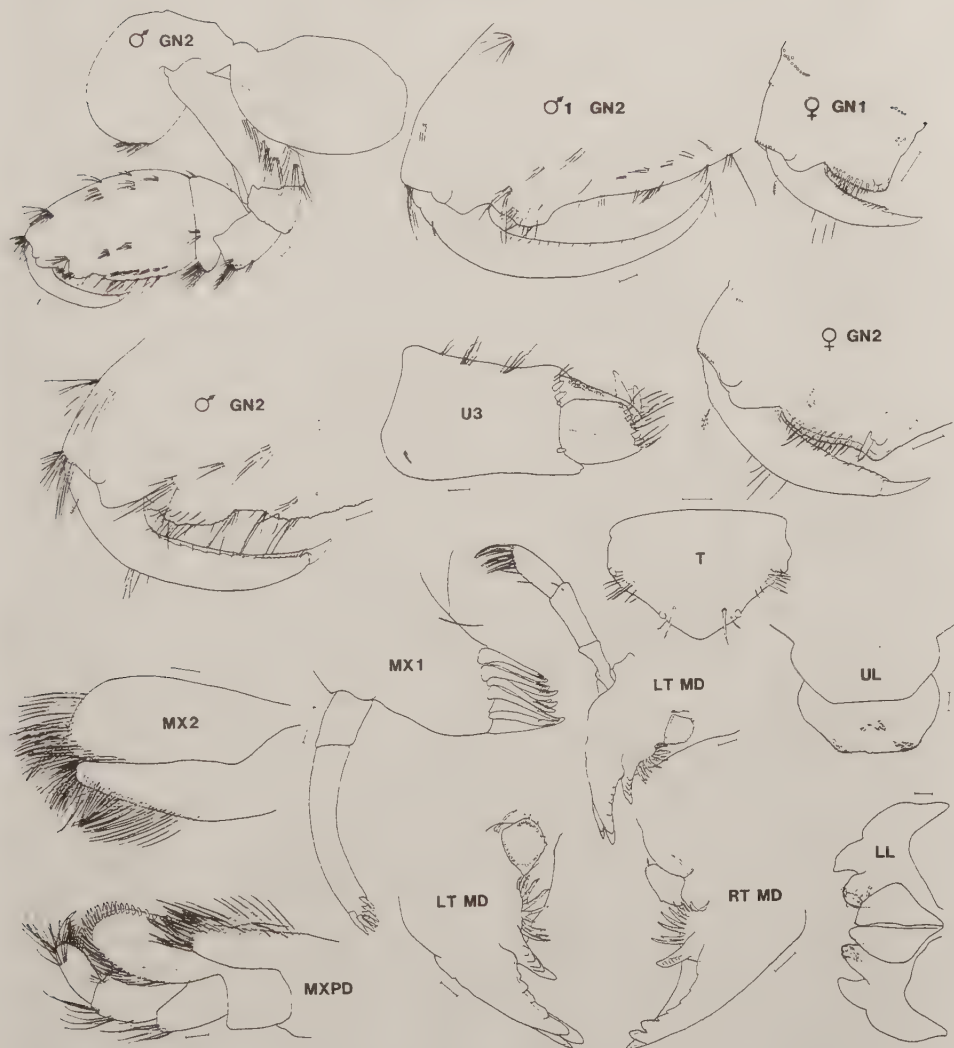


Fig. 2. *Peramphithoe stypotrumpetes*, new species. Holotype, female, 19.6 mm, Whitesboro Cove, Mendocino County, California, 28 February 1985, J. R. Chess, collector. Allotype, male, 13.1 mm, same location. Paratype, male 1, 15.8 mm, Big Branch Bay, Baranof Island, Alaska, 27 July 1980, J. R. Chess, collector. UL, upper lip; MD, mandible; LL, lower lip; MX, maxilla; MXP, maxilliped; GN, gnathopod; U, uropod; T, telson; RT, right; LT, left. Some gnathopod setae are not shown; their insertions are marked by a circle. Mouthparts are of the female. Scale bars 0.1 mm.

and 7, and left pereopods 5–7. Right gnathopod 2 slide-mounted; other appendages with carcass.

Variation.—Body length at maturity: male 12.1–13.1 mm, female 15.9–19.6 mm. The maturation length for the male is an assumption, because growth of the secondary

sexual characters is indeterminate and presence of penial papillae is not a reliable indicator of sexual maturity. Males of the sizes given above were found present with adult females and young. They are accordingly assumed to be the offsprings' parents, and therefore sexually mature. Second gnatho-



Fig. 3. Interior of a kelp stipe bored by *Peramphithoe stypotruripes*, showing the adult pair at top and three cohorts of offspring.

pod growth is indeterminate in all species of *Peramphithoe*; thus in males larger than those available for study here the dactyl may extend a greater distance along the posterior margin of the propodus.

Setae may be present or absent from the distolateral margin of the maxilla 1 palp.

Type Material.—HOLOTYPE, ♀ (Canadian Museum of Nature), catalogue no. NMCC1991-2120, and paratypes, 102 juveniles, catalogue no. NMCC1991-2123, Whitesboro Cove, Mendocino County, California, U.S.A. (39°13'N, 123°46.5'W), 28 February 1985, in 10-cm chamber bored in the stipe of *Laminaria dentigera* Kjellman, 1889, J. R. Chess, collector. ALLOTYPE, ♂ (Canadian Museum of Nature), catalogue no. NMCC1991-2121, and paratypes, 1 subadult ♀ and 1 juvenile, catalogue no. NMCC1991-2122, Point Cabrillo, Mendocino County, California (39°21'N, 123°49.5'W), 27 June 1980, in 3-cm chamber of *Laminaria dentigera*, J. R. Chess, collector. PARATYPES, 1 ♂, 1 adult ♀, and 156 juveniles, catalogue no. NMCC1991-2124, Santa Catalina Island, Los Angeles County, California (33°27'N, 118°29'W), 13 May 1980, in 31-cm chamber bored in the stipe of *Eisenia arborea* Areschoug, 1876, J. R. Chess, collector; paratype, 1 ♂, catalogue no. NMCC1991-2125, Whitesboro Cove, Mendocino County, 20 April 1981, from a stipe of *Laminaria dentigera*; paratypes, 1 ♂ and 1 adult ♀ brooding hatchlings, catalogue no. NMCC1991-2126, Big Branch Bay, Baranof Island, Alaska (56°03'N, 134°20'W), 27 July 1980.

Remarks.—All stages and both sexes of *Peramphithoe stypotrumpetes* can be distinguished quickly from *P. femorata* and other eastern Pacific species of *Peramphithoe* by the shorter first antenna. In *P. stypotrumpetes* the propodus of the female second gnathopod is larger relative to that of gnathopod 1 than it is in *P. femorata*. The palm of the second gnathopod propodus is shallowly concave in *P. stypotrumpetes* and transverse in *P. femorata*. In *P. stypotrumpetes* the bases of the third and fourth pereopods are narrower than those of other eastern Pacific species, and are very setose.

Four males, of 15.8, 13.9, 13.1, and 12.1-mm body length, were available for study, along with numerous small juveniles. Since two of these males were found cohabiting chambers with adult females and young, it is probable that they were sexually mature. However, their small size relative to that of the adult females suggests that they were not fully grown, since in other species of *Peramphithoe* the adult male achieves a larger size than the adult female.

Etymology.—The name is formed from the Greek words “*stypos*,” meaning stalk, and

“*trumpetes*,” meaning borer, referring to the species' habit of boring in kelp stipes.

Habits of Peramphithoe stypotrumpetes.—Ecological observations were made by one of us (JRC) along exposed parts of the Pacific coast of North America. *Peramphithoe stypotrumpetes* was found in the stipes of *Eisenia arborea* in southern California (Santa Catalina Island) and in stipes of *Laminaria dentigera* in northern California (Mendocino County) and southeastern Alaska (Baranof Island). Specimens probably referable to this species have been found in the stipes of *Pterygophora californica* Ruprecht, 1852, in southern California (Steve Schoeter, University of California, Santa Barbara, personal communication).

Peramphithoe stypotrumpetes feeds on the inner stipe tissues, as shown by microscopic examination of gut contents. The amphipod consumes tissues of the transition zone, medulla, and cortex of a stipe, which destroys the plant's ability to regenerate fronds and eventually leads to its death.

Infestation of the algae occurs when a single *Peramphithoe stypotrumpetes*, male or female, bores into the stipe at its distal end (refer to Fig. 3). Every observed entry was into a stipe whose fronds had been abraded away by physical or biotic forces. The following summary is based on examination of 74 stipes in various stages of infestation. After hollowing the stipe to a depth of 2–6 cm, the original invader is joined by another of the opposite sex. These mate and continue to bore deeper into the stipe, hollowing it as they go. By the time the first brood of juveniles is released, the adults have bored out a chamber of 4–8 cm depth. Often by the time the first cohort has grown to 2 mm, a second cohort is being brooded by the female. Successive cohorts remain in the chamber, all grazing on the stipe's interior. Usually by the time the chamber is 5–10 cm deep, the amphipods have bored small pores (1–3 mm diameter) through the stipe wall. As the amphipods continue to multiply, their chamber grows larger and the number of perforations increases. During this time the distal end of the stipe begins to disintegrate, so that as the chamber lengthens the stipe shortens. The amphipods leave the stipe when it has been completely hollowed out or when its inner tis-

sues have begun to decompose. Often in northern California a few *Jassa staudei* Conlan, 1990, occur among *P. stypotrupetes* in the chambers of the older, disintegrating stipes.

In most of the infested stipes examined, the larger chambers contain more amphipods than do the smaller, but this relation fails to hold with extremes of either variable. Thus, the deepest chamber, 52 cm, contained only three subadults, and the largest number of amphipods, 208, occurred in a chamber only 14 cm deep. This larger group included two adults (a 19-mm male and a 24-mm female) and three distinct sibling cohorts, 103 individuals 2–3 mm long, 49 at 5–7 mm, and 54 at 9–11 mm (refer to Fig. 3).

Peramphithoe femorata (Krøyer, 1845)
Figs. 1, 4

Ampithoe femorata Krøyer, 1845, 335, pl. 3, fig. 4.
Peramphithoe femorata: Conlan and Bousfield, 1982,
68, 69, fig. 16.

Ampithoe brevipes Dana, 1852, 216.

Adult Female.—Lectotype (here designated): Body length 20.8 mm. Body stout, head not bulbous. Eye small. Antenna 1, peduncle overlapping 75% of antenna 2 peduncular article 4; peduncular article 1 without spine at posterodistal corner; article 2 98% of length of article 1. Antenna 2, flagellum moderately setose, proximal articles fused. Mandible, lacinia mobilis with 7 teeth left, 13 teeth right, raker spines 12 left, 14 right; palp article 3 with setae on distal margin only. Maxilliped, palp article 4, width 76% of article 3 width. Gnathopods 1 and 2 and pereopods 3 and 4, bases moderately setose posteriorly only. Gnathopod 1, carpus 93% of propodus length; dactyl extending beyond palm of propodus by 40% of its length. Gnathopod 2, propodus maximally 140% of width of propodus of gnathopod 1, palm transverse. Pereiopod 3, basis 220% of width of basis of gnathopod 2, width 60% of length; merus, width 175% of width of carpus. Pereiopod 5, basis, width 114% of length. Pereiopod 7, length 117% of pereiopod 6; bases posterodistally concave; propodus with 9 spine groups. Uropods 1 and 2, rami slender and densely spinose. Uropod 3, peduncle 1.5 times length of rami.

Condition.—Not brooding. With all appendages. Antennae 1, flagellar tips absent.

Adult Male.—Not type. Canadian Museum of Nature, accession no. 70–218, station no. 27896, Cape Horn Island, Chile, J. Markham, collector, 1970. Length 15.8 mm. Gnathopod 2, propodus, palm with shallow tubercle proximal to dactyl insertion and indentation proximal to tubercle; dactyl extending through 68% of length of propodus, palmar defining spine absent.

Condition.—Without antennae 1 and 2 or pereopods 5–7. Right appendages, mouthparts, and telson slide-mounted. Left appendages with carcass.

Variation.—Body size at maturity: male 15.8 mm, female 20.8 mm. The maturation size for the male is an assumption, because growth of the secondary sexual characters is indeterminate and the presence of penial papillae is not a reliable indicator of sexual maturity. In the 11.5-mm male, the palm of the propodus of the second gnathopod lacks a tubercle proximal to the dactyl insertion. There is a defining spine at the palmar corner.

Type Material.—Lectotype (here designated), adult ♀, 20.8 mm, Universitets Zoologiske Museum København; Valparaíso, Chile (33°05'S, 71°40'W). Paralecotypes, 3 juveniles, same location.

Other Material (excluded from type series).—Two ♂♂ and 1 subadult ♀, Cape Horn Island, Chile (56°S, 67°W), 1970, Canadian Museum of Nature accession no. 70–218, station no. 27896; 4 juvenile ♂♂, 1 juvenile ♀, Banco de las Tacas, Isla Navarino, Chile (55°05'S, 67°04'W), 5 February 1970, Canadian Museum of Nature accession no. 70–218, station no. 27924, J. Markham, collector.

Remarks.—The 15.8-mm and 11.5-mm males illustrated in Fig. 4 were illustrated in Conlan and Bousfield (1982), but their body lengths were given erroneously as 18.0 mm and 12.5 mm, respectively. Like *Peramphithoe humeralis*, *Peramphithoe femorata* builds tubes among kelp fronds. The living habits of *P. femorata* are described by Kreibohm de Paternoster and Escofet (1976) and Kreibohm de Paternoster (1985).

Species Relationships

Cladistic Analysis.—Characters used for cladistic analysis are listed in Appendix Table 1. Their raw states are shown in Appendix Table 2, and the gap-coded states are given in Appendix Table 3. For nine

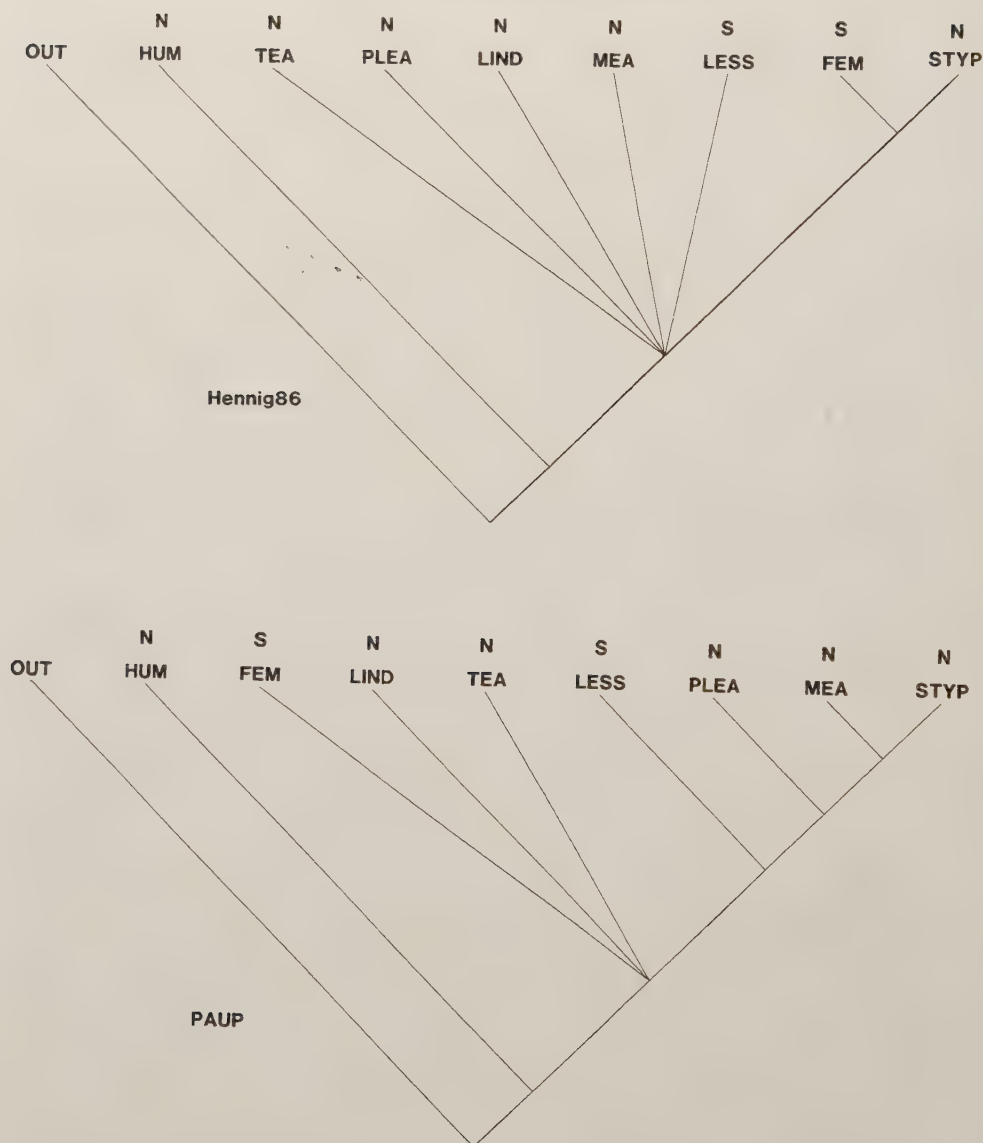


Fig. 5. Above: Nelson consensus tree produced by the cladistics program Hennig86. Below: Nelson consensus tree produced by the cladistics program PAUP. In each case the distribution is indicated as N, North America; S, South America. Abbreviations: OUT, outgroup (*Ampithoe lacertosa*); HUM, *P. humeralis*; TEA, *P. tea*; PLEA, *P. plea*; LIND, *P. lindbergi*; MEA, *P. mea*; LESS, *P. lessoniophila*; FEM, *P. femorata*; and STYP, *P. stypotruripes*.

such as *Peramphithoe*, the greatest evolutionary forces have been on the body appendages that extend from the tube.

Wagner analysis using Hennig86 produced 28 trees of length 46. The Nelson consensus tree for the eight species of *Per-*

amphithoe (outgroup species deleted) is shown in Fig. 5a. The character consistency index for the consensus tree is 60 and the retention index 33. The consensus tree shows an unresolved polychotomy for the north-eastern Pacific *Peramphithoe tea*, *P. plea*, *P.*

lindbergi, and *P. mea*, and the southeastern Pacific *P. lessoniophila*. *Peramphithoe stypotrumpetes* is grouped with *P. femorata*.

Wagner analysis using PAUP produced three trees of length 23.25. The Nelson consensus tree is shown in Fig. 5b. Rohlf's consistency index for the consensus tree is 0.679. The consensus tree is not fully resolved, with *P. femorata*, *P. lindbergi*, and *P. tea* forming a trichotomy. In this case, the sister species to *P. stypotrumpetes* is *P. mea*.

It is apparent from both cladistic analyses that the eastern Pacific species of *Peramphithoe* closely resemble each other, and that the fifteen characters found to differentiate the species are not very congruent. The only consistencies in the two consensus trees are the positions of *P. humeralis* and *P. stypotrumpetes*.

Biogeography.—All species of *Peramphithoe* are restricted to cold temperate waters. An allopatric speciation event can be hypothesized for both phyletic scenarios for *Peramphithoe stypotrumpetes*. In the Hennig86 scenario the proposed sister species is *P. femorata*, a species that is endemic to southern Chile, and thus is well separated from *P. stypotrumpetes* by tropical waters. In the PAUP scenario, the proposed sister species is *P. mea*, the most northwesterly ranging species of the genus, occurring in the Aleutian Islands and the Sea of Japan. Undoubtedly *P. stypotrumpetes* will be found in other parts of the eastern Pacific within its currently documented range of California to southeastern Alaska. American endemic species with such ranges do not generally occur as far north as the Aleutian Islands, however (Bousfield, 1979, 1982; Conlan and Bousfield, 1982; Conlan, 1983). Thus, *P. stypotrumpetes* is probably well separated in its range from *P. mea*, and could have evolved allopatrically from a common ancestor.

KEY TO EASTERN PACIFIC SPECIES OF PERAMPHITHOE

(After Conlan and Bousfield (1982), in which all eastern Pacific species but *Peramphithoe stypotrumpetes* are illustrated.)

1. Antenna 2, flagellum, proximal articles not fused (first article twice or less length of following 2 articles, without any more setal clusters than on following articles). Adult male gnathopod 2, propodus, width less than twice width of propodus of gnathopod 1 2
- Antenna 2, flagellum, proximal articles fused (first article more than twice length of following articles and with more setal clusters than on following articles). Adult male gnathopod 2, propodus, width more than twice width of propodus of gnathopod 1 3
2. Gnathopod 1, carpus longer than propodus. Gnathopod 2 (both sexes), propodus hardly larger than that of gnathopod 1, palm transverse; carpus longer than deep, and as long as propodus. Pereiopod 7 about 1.5 times length of pereiopod 6. Central Alaska to Baja California. *Peramphithoe humeralis* (Stimpson, 1864)
- Gnathopod 1, carpus as long as propodus. Gnathopod 2 (both sexes), propodus larger than that of gnathopod 1, palm oblique; carpus shorter than deep and shorter than propodus. Pereiopod 7 less than 1.2 times length of pereiopod 6. Aleutian Islands, Alaska, and Japan Sea. *Peramphithoe mea* (Gurjanova, 1938)
3. Antenna 1 about as long as antenna 2. Pereiopods 3 and 4, bases, width 1.5 times width of basis of gnathopod 2. Boring into and inhabiting kelp stipes *Peramphithoe stypotrumpetes*, new species
- Antenna 1 about 25% longer than antenna 2. Pereiopods 3 and 4, bases, width more than 1.5 times width of basis of gnathopod 2. Tubicolous, in algal fronds 4
4. Body length at adulthood 12–35 mm. Southern hemisphere *Peramphithoe femorata* (Krøyer, 1845)
- Body length at adulthood 6–13 mm. Mainly northern hemisphere 5
5. Male gnathopod 2, propodus 2 times width of propodus of gnathopod 1, palm shallowly concave, dactyl less than half length of posterior margin. Southern hemisphere *Peramphithoe lessoniophila* Conlan and Bousfield, 1982
- Male gnathopod 2, propodus 3 times width of propodus of gnathopod 1, palm concave or transverse, dactyl half or more length of posterior margin. Northern hemisphere 6
6. Antenna 1, peduncle article 3 without posterodistal spine. Antenna 2 slender and nearly as long as antenna 1. Gnathopod 1, propodus, dactyl overlapping palm by hardly more than length of unguis. Male gnathopod 2, propodus rectangular, palm with tubercle at dactyl hinge, dactyl sinuous *Peramphithoe plea* (Barnard, 1965)
- Antenna 1, peduncle with posterodistal spine in adults. Antenna 2 heavy, less than three-quarters length of antenna 1. Gnathopod 1, propodus, dactyl overlapping palm by more than length of unguis. Male gnathopod 2, propodus wider proximally than distally, palm with or without tubercle at dactyl hinge, dactyl evenly curved 7
7. Antenna 2 about three-quarters length of antenna 1; flagellum about 1.5 times length of peduncular article 5, proximal articles of flagellum fused in pairs. Male gnathopod 2, prop-

odus, palm with tubercle at dactyl hinge, dactyl reaching length of palm in larger individuals
Peramphithoe tea (Barnard, 1965)
 Antenna 2 about half length of antenna 1; flagellum about as long as peduncular article 5, proximal 5 and 6 articles of flagellum fused. Male gnathopod 2, propodus, palm without tubercle at dactyl hinge, dactyl half or less length of palm
Peramphithoe lindbergi (Gurjanova, 1938)

DISCUSSION

Although all species of the genus *Peramphithoe* are herbivorous, *P. stypotrupetes* is the only species known to bore into kelp stipes. Other species of the genus colonize algae, living within tubes, channels gouged along tissue edges, or rolls of algal blades cemented together with self-produced "amphipod silk" (Griffiths, 1979; Gunnill, 1984). They eat the surrounding algae (as in *P. humeralis* (see Jones, 1971; Griffiths, 1979)), or consume drift and/or epiphytic algae (as in *P. tea* (see Gunnill, 1982)).

The living habits of *Peramphithoe stypotrupetes* differ from other members of the genus and are reflected in a somewhat altered morphology. The head is rather bulbous, the antennae are short and about equal in length, the body is stout, and pereopod 3 and 4 bases, which house the silk-secreting glands, are not as expanded as in other (at least eastern Pacific) members of the genus. Species of *Peramphithoe* do not achieve as great a diversity of sexual dimorphism in the second gnathopods as do species of *Ampithoe*. This suggests that sexual habits differ between the genera, perhaps trending toward monogamy in some species of *Peramphithoe*. This appears to be the case, at least, for *P. stypotrupetes*.

Generally, species of *Peramphithoe* have larger pereopod bases which house the web-spinning glands than do species of *Ampithoe*. Species of *Ampithoe* build their tubes among eelgrass, kelp holdfasts, coralline algae, and such green, brown, and red algae as *Ulva*, *Enteromorpha*, *Monostroma*, *Spongomorpha*, *Codium*, *Chordaria*, *Ralfsia*, *Dictyota*, *Sargassum*, *Fucus*, *Pelvetia*, *Leathesia*, *Halidrys*, *Cystoseira*, *Padina*, *Desmarestia*, *Polysiphonia*, *Chondrus*, *Gracillaria*, *Gracillariopsis*, *Neoagardhiella*, *Polyneura*, *Callophyllis*, *Prionitis*, *Antithamnion*, *Amphiroa*, *Rhodymenia*, *Rhodomela*, *Ceramium*, *Iridaea*, *Schizymenia*,

Cladophora, *Halosaccion*, *Jania*, *Laurencia*, *Peyssonellia*, *Cryptonemia*, *Calonitophyllum*, *Chondria*, and *Hypnea* (Holmes, 1901; Skutch, 1926; Shoemaker, 1938; Heller, 1968; Barnard, 1969, 1970; Nicotri, 1977; Bellan-Santini *et al.*, 1982; Conlan and Bousfield, 1982; Moore, 1984; Myers, 1985; Hay *et al.*, 1987; Duffy and Hay, 1991). Species of *Peramphithoe* occur on the branching brown alga *Pelvetia* and the blades and holdfasts of such large kelps as *Laminaria*, *Macrocystis*, *Agarum*, *Egregia*, *Lessonia*, and *Ecklonia* (Barnard, 1969; Jones, 1971; Griffiths, 1979; Conlan and Bousfield, 1982; Gunnill, 1982, 1983, 1984; Kreibohm de Paternoster, 1985), or in the stipes of *Eisenia*, *Laminaria*, and *Pterogophora* (*Peramphithoe stypotrupetes*, this study). This affinity for larger and tougher algae suggests that species of *Peramphithoe* are more powerful algal manipulators than are species of *Ampithoe*.

Peramphithoe stypotrupetes is not unique within the family Ampithoidae in its burrowing habits. In Britain, *Amphitholina cuniculus* (Stebbing, 1874) burrows into the medullary region of stipes of the kelp *Alaria esculenta* (Linnaeus) Greville, 1830 (Myers, 1974). Like *P. stypotrupetes*, *A. cuniculus* burrows extensively and perforates the stipe in numerous places. *Amphitholina cuniculus* has never been found with more than six conspecifics in a stipe chamber, however. *Amphitholina cuniculus* is much more modified for burrowing than is *P. stypotrupetes*. Its mouthparts are prognathous and styliform. The head is beaked in appearance, and dorsally grooved, presumably to accommodate the antennae during burrowing. There are several taxa of amphipods outside the family Ampithoidae that burrow. Members of the corophioidean family Cheluridae burrow into timber and can be destructive to pilings and moorings (Holmes, 1905). Members of the corophioidean family Biancolinidae burrow into kelp stipes in tropical and semitropical waters. As with *Amphitholina*, their heads are globose and their mouthparts prognathous (Myers, 1985). Members of the talitrid families Najnidae, Phliantidae, and Eopliantidae burrow into kelp stipes in a fashion similar to *P. stypotrupetes*.

In tube-building corophioidean amphipods, with which *Peramphithoe stypotru-*

petes is classified, the adult male usually leaves his mate's tube following mating, and the activities of the mother and her new partner cause the young to leave as well (Borowsky, 1983; Shillaker and Moore, 1987). In *P. stypotruripes*, the regular collection of a mating pair with offspring suggests a prolonged period of residency for all concerned, at least until the chamber erodes sufficiently for it to be abandoned. The difference in living habit may be related to the substance of the housing structure. In most other tubicolous amphipods the housing material consists of detritus, wood debris, shells, algal cuttings, or fronds wrapped around the body and glued in place with "amphipod silk." For *P. stypotruripes* the housing is also the food source, and consumption of the stipe interior generates added space for new offspring. There is, therefore, not as immediate a housing-size limitation as might be experienced by tube-dwellers whose housing does not enlarge on demand.

Brood care and prolonged cohabitation are not common among amphipods, but do occur in a few other species. Bate and Westwood (1863) found cohorts of two sizes of *Podocerus variegatus* Leach, 1814, cohabiting a tube. Mothers and their offspring of the podocerids *Dulichia rhabdoplastis* McCloskey, 1970, *Dyopedos porrectus* Bate, 1857, and *Dyopedos monacanthus* (Metzger, 1875) live on self-built rodlike structures attached to the ends of sea urchin spines, hydroids, bryozoans, or shells (McCloskey, 1970; Moore and Earll, 1985; Mattson and Cedhagen, 1989). Females of *Caprella monoceros* Mayer, 1890, carry their young with them after release from the brood pouch, grooming them and defending them from other caprellids (Aoki and Kikuchi, 1991). Young *Leptocheirus pilosus* Zaddach, 1844, remain in the mother's tube until at least the second molt (Goodhart, 1939). *Phronima sedentaria* Forskål, 1775, rears young in hollowed out salp or pyrosome barrels (Hardy, 1956; Laval, 1980). *Peramphithoe humeralis*, which rolls kelp fronds and occupies the chambers so formed, lives in a manner similar to *P. stypotruripes*. Young cohabit the chamber and feed on the inner wall of the distal end, progressively extending the chamber backward as the walls are eaten (Griffiths, 1979), or leave en masse on foraging forays elsewhere (Jones, 1971).

Peramphithoe tea, found in the fucoid alga *Pelvetia fastigiata* (J. Agardh, 1841) DeToni, 1895, also appears to reproduce as a colony (Gunnill, 1982).

The phyletic relationship of *Peramphithoe stypotruripes* to eastern Pacific members of the genus is not well resolved. The phyletic scenarios developed by the cladistics programs employed here set closest relationships to species that are well separated from *P. stypotruripes* geographically. Species of *Peramphithoe* are not as highly sexually dimorphic as are species of *Ampithoe*, and somatic characters are not highly variable. The greatest differences between the species of *Peramphithoe* may be in their feeding habits and substrate preferences, both of which require further investigation.

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A BIOECONOMIC MODEL OF THE PACIFIC WHITING*

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The Pacific whiting (*Merluccius productus*) is a highly migratory fish occupying the continental shelf and slope off the west coast of North America. The species spawns in January off southern California and northern Mexico. During spring and summer the older and larger fish will migrate as far north as central Vancouver Island. Recruitment is highly variable, with strong year classes often supporting the commercial fishery during several years of low recruitment. The level of recruitment appears to be independent of the size of the spawning population.

A simple bioeconomic model of the Pacific whiting is constructed with independent recruitment. Fishery production functions are estimated from data on U.S. catch, average annual biomass and the number of vessels in the U.S. fleet. A stochastic optimization problem, seeking to maximize the expected value of industry profit, is formulated. Its solution would require a joint distribution on future recruitment and other bioeconomic parameters. Such a distribution is problematic. As an alternative, the certainty-equivalent problem is solved yielding solution values for the stochastic equilibrium and an approximately-optimal rule that sets allowable catch based on an estimate of current-year biomass.

Adaptive management can result in large changes in fleet size and allowable catch from year to year. The whiting fishery might be characterized as an opportunistic fishery, requiring a generalist fleet to expand or contract as bioeconomic conditions warrant. It is possible that long-run conditions would not support a profitable fishery, but that short-run fishing is profitable based on previous years of strong recruitment. The situation is not dissimilar to that facing the owner of a marginal gold mine that opens or closes depending on the price of gold. In the case of the whiting fishery, the optimal level of short-run fishing will depend not only on price, but on current biomass, the annual cost of fishing, the discount rate and vessel productivity. A simple interactive program is provided for would-be managers.

1. Introduction. With the development of a joint-venture fishery, the Pacific whiting (*Merluccius productus*) has become a commercially valuable species. Trawlers from California, Oregon, Washington and the province of British Columbia harvest whiting (also called hake) and then off-load the cod-end of their nets to a foreign factory vessel where the whiting is quickly processed to preserve freshness and texture. In 1989, the U.S. fleet delivered approximately 204 000 metric tons of whiting to foreign processing vessels, earning about \$21 million in revenues.

The Pacific whiting is a highly migratory species, spawning off the coasts of southern California and northern Mexico in January (Bailey *et al.*, 1982).

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During the spring and summer the population migrates northward, with the older and larger fish crossing into Canadian waters in August. Joint-venture arrangements have proved profitable to both U.S. and Canadian trawlers, and the distribution of allowable catch between the U.S. and Canada has taken on greater importance. While there is no formal treaty, fisheries managers from both countries have met to work out a long-term plan for binational allocation.

Recruitment in the whiting fishery appears to be independent of spawning biomass, but is positively correlated to surface temperature during spawning. Temperature in the month of January is affected by Eckmann transport, a process where warmer nearshore surface waters are pushed offshore, followed by an upwelling of deeper, cooler water (Bailey, 1981).

By August the whiting stock is distributed along the coast by age. While the location of a cohort in a particular year will depend on temperature, cohorts aged two to six are likely to be found off northern California and Oregon, while cohorts 7 to 14 are likely to be found off the coasts of Washington and British Columbia. In September and October whiting begin their southward migration from the feeding grounds to the spawning areas, and the cycle repeats itself.

The age structure of the resource and its reasonably stable migratory pattern have lead previous researchers to develop cohort models with population dynamics, migration and trophic interactions (Francis, 1983), stochastic recruitment (Swartzman *et al.*, 1983), and a game-theoretic approach to U.S.-Canadian management (Swartzman *et al.*, 1987). Dorn and Methot (1989) also employ a cohort model with recruitment randomly generated by iterative resampling from estimates of recruitment for the period 1959-1986. Constant and variable effort strategies are examined by averaging yields from 10 replicate, 1000-year simulations. Estimates of average yield ranged from 178 000 to 244 000 tons for the constant-effort strategy and from 205 000 to 251 000 tons for the variable-effort strategy. They recommend that total allowable catch be split 80 and 20% for the U.S. and Canada, respectively.

A simpler approach is taken in this paper. All the numerical results can be derived from the nine observations on catch, mean annual biomass and effort (vessel numbers) in Table 1, and by using the 20-line program (in BASIC) listed in Table 3. Analytical expressions for stochastic equilibrium and the approximately-optimal policy rule for adaptive management require some calculus and a fair amount of tedious algebra.

While the model is simple, it incorporates economic elements which have been absent in all the previous modeling of the Pacific whiting. Specifically, the program in Table 3 will employ estimates of a vessel productivity parameter, natural mortality, annual cost per vessel, dockside (or exvessel) price, the real rate of discount (interest) and long-run average recruitment to calculate what

has been called the stochastic equilibrium. More relevant to short term management is the adaptive-management rule which, given an updated set of bioeconomic parameters and an estimate of current-year biomass, will suggest levels for allowable catch and fleet size. The issue of distributing allowable catch between the U.S. and Canada is left for resolution by managers from both countries.

The rest of this paper is organized as follows. In the next section we construct a bioeconomic model and derive equations defining stochastic equilibrium and the adaptive-management rule. In the third section we estimate production functions for the Pacific whiting fishery and calibrate the model for price and cost *circa* 1988. Section 4 examines stochastic equilibria and the performance of the adaptive-policy rule for allowable catch under a range of values for the bioeconomic parameters. The paper concludes with a discussion of the implications and limitations of the model.

2. Bioeconomics: Stochastic Equilibrium and Adaptive Management. Let X_t denote the average biomass of Pacific whiting in year t , E_t the level of fishing effort in year t and Y_t the level of harvest or catch. We assume there exists a production function relating annual catch to biomass and effort and write $Y_t = F(X_t, E_t)$, where the partial derivatives of $F(X_t, E_t)$ are denoted with subscripts and assumed to have the following signs: $F_X > 0$, $F_E > 0$, $F_{X,E} = F_{E,X} > 0$, $F_{X,X} \leq 0$ and $F_{E,E} \leq 0$. If p denotes the exvessel price per unit of catch (say, \$/metric ton) and c the cost of effort (say, cost/vessel/year), then we may write net revenue or profit in year t as:

$$\pi_t = pF(X_t, E_t) - cE_t. \quad (1)$$

Average annual biomass is assumed to change according to the following first-order difference equation:

$$X_{t+1} = (1 - M)[X_t - F(X_t, E_t)] + R_t \quad (2)$$

where M is annual natural mortality and R_t is a random variable denoting recruitment in year t . Maximization of the present value of expected profits subject to the dynamics of mean annual biomass may be stated mathematically as:

$$\text{Maximize } E \left\{ \sum_{t=0}^{\infty} \rho^t [pF(X_t, E_t) - cE_t] \right\}$$

$$\text{Subject to } X_{t+1} = (1 - M)[X_t - F(X_t, E_t)] + R_t$$

where $\rho = 1/(1 + \delta)$ is a discount factor and δ is the real rate of discount (or real annual interest rate).

This stochastic optimization problem might be solved by dynamic programming if a distribution for future recruitment were known. If other bioeconomic parameters are also random variables then one would need a joint distribution over all random variables. Such a distribution is problematic. As an alternative we consider what is called the "certainty-equivalent problem". The name is a bit of a misnomer, because the solution to the certainty-equivalent problem will not be the same as the solution to the stochastic dynamic programming problem (when the necessary distribution is known). The actual degree of suboptimality associated with the solution to the certainty-equivalent problem will depend on the specifics of the problem, the functional forms, the presence of irreversibilities, and the degree to which initial conditions differ from the long-run "stochastic equilibrium".* Before discussing the issue of suboptimality further, it may be useful to pose and solve the certainty-equivalent problem.

Let the expected value of R_t be denoted by R . The certainty-equivalent problem is the deterministic problem obtained by substituting the expected value for its random variable. This results in a problem with a Lagrangian expression that may be written as:

$$L = \sum_{t=0}^{\infty} \rho^t \{ pF(X_t, E_t) - cE_t + \rho\lambda_{t+1} [(1-M)[X_t - F(X_t, E_t)] + R - X_{t+1}] \} \quad (3)$$

where λ_{t+1} is the Lagrange multiplier associated with biomass in period $t+1$, and may be interpreted as the marginal value of an additional unit (say, metric ton) of fish in the water in year $t+1$. The Lagrange multiplier is also called the "shadow-price" of the fish stock. Note that R becomes a parameter in the certainty-equivalent problem.

In the Appendix we derive the first-order necessary conditions for this problem. They can be evaluated in steady state and are shown to imply the following two equations:

$$\frac{c(1-M)F_X}{(pF_E - c)} = \delta + M \quad (4)$$

$$R = MX + (1-M)F(X, E). \quad (5)$$

Equation (4) is a special case of what has been called the "fundamental equation of renewable resources" (see Conrad and Clark, 1987, p. 34). With independent recruitment the first derivative of the net growth function vanishes

* Perhaps a more accurate name would be "certainty-equivalence equilibrium" since the concept of stochastic equilibrium is usually associated with a stationary probability distribution.

and we are left equating the "marginal stock effect" to the sum of the rate of discount and natural mortality. The marginal stock effect measures the incremental cost savings from larger biomass relative to the immediate benefit if that increment in biomass were harvested this year.

Equation (5) requires that expected (or long-run average) recruitment offset the reduction in biomass from natural mortality plus that portion of biomass that would have survived had it not been harvested. Equations (4) and (5) collectively define what Burt (1967) refers to as the stochastic equilibrium. Burt was concerned with the optimal management of a groundwater stock when recharge (from rain or melting snow) was stochastic. He notes that the stochastic equilibrium is "always approached, but rarely experienced".

The stochastic equilibrium for our problem is portrayed in Fig. 1. From the implicit function theorem, equation (4) will define a curve in $X-E$ space. Totally differentiating equation (4) and making use of the partials of $F(X, E)$, we can show that along this curve dE/dX is positive. Depending on the form of $F(X, E)$ it may be possible to solve for an explicit relationship, $E = E(X)$, that is positively sloped.*

Equation (5) also implies a curve in $X-E$ space. Total differentiation and the signs for F_X and F_E will imply that along this curve $dE/dX < 0$. If an explicit relationship, $E = R(X)$, can be obtained from equation (5), it will be negatively sloped. Thus, the partials of $F(X, E)$ imply that a nonzero stochastic equilibrium, (X_R, E_R) in Fig. 1, will be unique.

While the stochastic equilibrium may be of interest in determining the long-run effects of changes in the bioeconomic parameters, it is not very useful for short-term management. When fish biomass is not at its long-run equilibrium we would need to solve the deterministic certainty-equivalent problem, or a finite-horizon stochastic dynamic programming problem to determine the first step along an "approach path". With $F(X_t, E_t)$ nonlinear, this is not a trivial problem.

Instead of taking this tack we make use of an "approximately-optimal" technique proposed by Burt (1964, 1967) for groundwater management and more recently examined by Kolberg (1990) for management of a fishery. This approach makes use of equation (4) by noting that it can be regarded as defining a relationship between X_t and E_t in the vicinity of long-run equilibrium. Could we use this relationship for short-run management? If we do, how inferior would the resulting decisions be, relative to the solution

* The curve $E(X)$ has nothing to do with the expectation operator. It is a smooth, positively-sloped curve obtained from equation (4) and will be used to identify the approximately optimal level of effort given an estimate of biomass, X . The curve implied by equation (5) will be denoted $E = R(E)$, since this curve will depend on parameters of the production function, the annual mortality rate and the long-run, expected level of recruitment, R . This latter curve is used in defining the stochastic or certainty-equivalence equilibrium, but only $E(X)$ is needed for short-run, adaptive management.

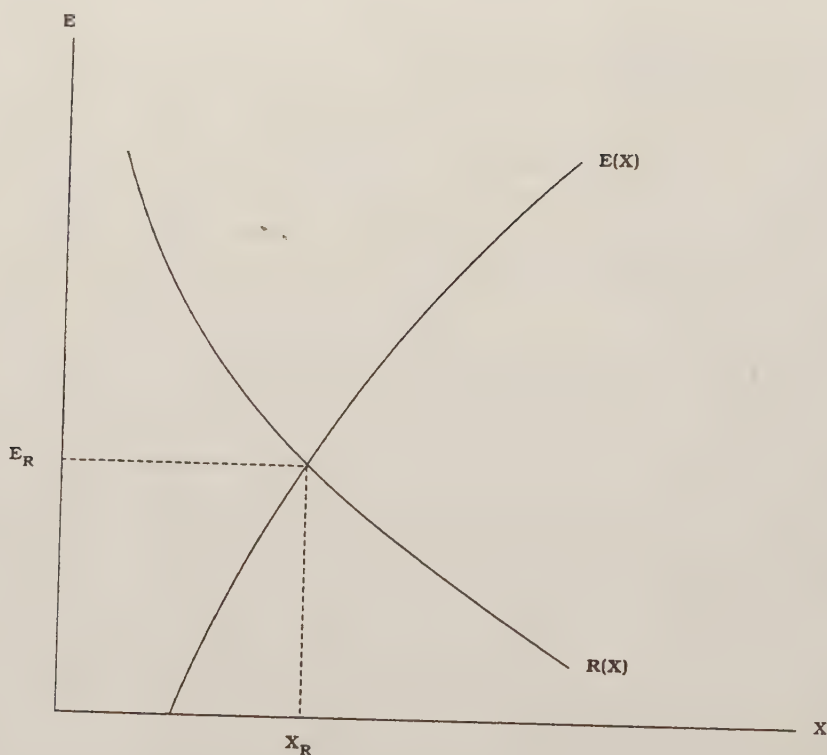


Figure 1. The long-run stochastic equilibrium.

obtained for a stochastic dynamic programming problem (with a known distribution for recruitment)? We will take these two questions in order.

The procedure for using equation (4) as an adaptive management rule is shown in Fig. 2. In the northeast quadrant we have redrawn the $E(X)$ curve from Fig. 1. Its position depends on all of the bioeconomic parameters except R , expected recruitment, which only appeared in equation (5). Suppose that biologists, using data from a series of scientific trawls or through a cohort model taking into account last year's total (U.S. plus Canadian) harvest, could provide managers with an estimate of biomass for the forthcoming year. With an estimate of X we could project up to the $E(X)$ curve to determine the recommended level of effort. The estimate of current biomass will also imply a specific production function in $E-Y$ space drawn in the northwest quadrant. Projecting E over to the appropriate production function results in a catch rate which might be used as allowable catch for the forthcoming year. Because recruitment is stochastic and because fishermen may exceed or fail to harvest allowable catch in a particular year, the subsequent estimates of X may bounce around. From Fig. 2 we can get a qualitative feel for how recommended effort

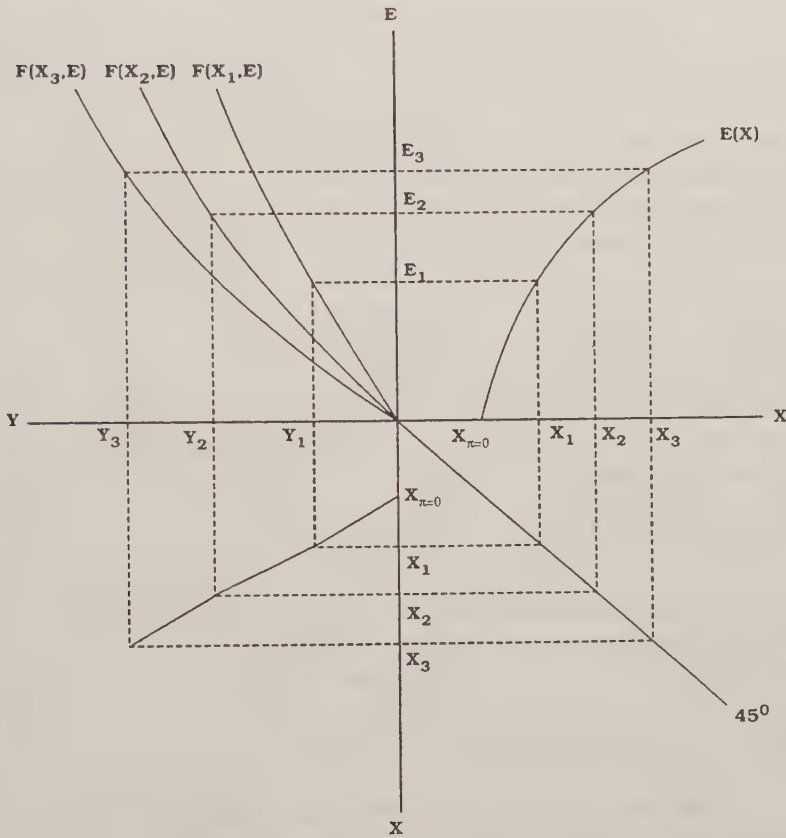


Figure 2. A depiction of the approximately-optimal feedback policy.

and allowable catch vary with X . First, note that there is likely to be an intercept of the $E(X)$ curve on the X axis. This has a straightforward interpretation. For a given set of bioeconomic parameters (per unit price, annual cost, the rate of discount, natural mortality, and perhaps catchability) there is likely to be some stock level below which fishing today would reduce present value. This is denoted by $X_{\pi=0}$. As X increases we see a less than proportional increase in E . The resulting change in Y is less easy to assess qualitatively because the production function shifts upward with increases in X . With a particular form for $F(X, E)$, and given estimates of the bioeconomic parameters, we could numerically examine the change in Y for a change in X . (We will do this for the whiting fishery in Section 4.) If we wish, we could collect the (X, Y) pairs by constructing a 45° transfer line in the southeast quadrant, project X downward, across, and then pair it with the corresponding Y projected downward from the Y -axis of the northwest quadrant. This is done in

the southwest quadrant and the four "dots" have been (arbitrarily) "connected" by a series of line segments.

Burt compared the level of groundwater pumping recommended by such a procedure to the level of pumping recommended when using stochastic dynamic programming, taking the estimate of current X as an initial condition, with all other parameters the same. In his study he found that the pumping rates differed by less than 2% when the current groundwater stock was within 42% of the stochastic equilibrium. As the current stock got closer to the stochastic optimum, the difference went to zero. On the basis of this relatively small departure from the optimal pumping rate, Burt dubbed this rule "the approximately-optimal" pumping rule.*

Burt and Cummings (1977), in considering this rule for other renewable resources, found that the difference between the approximately-optimal harvest rate and the optimal rate obtained via stochastic dynamic programming was likely to exhibit a consistent and perhaps attractive bias. When $X < X_R$ the harvest rate from the approximate rule was likely to be less than the harvest rate from the optimal rule. When $X > X_R$ harvest was likely to be slightly more than optimal. This would lead to a more rapid approach to equilibrium in a deterministic model. The slightly lower levels for recommended harvest when the resource stock was less than its stochastic equilibrium caused Burt and Cummings to regard the approximate rule as also being "conservative". Managers may find this built in conservatism (when stock is low) to be attractive.

In a recent study and application to the anchovy fishery in northern California, Kolberg (1990) analyzed the above approximate procedure and compared it to the optimal solution (obtained via dynamic programming) and two other approximate solutions obtained from first- and second-order Taylor approximations to the value function at the steady state optimum. Burt's original approximate rule [equation (4) in this paper] is equivalent to the first-order approximation of the value function. Kolberg finds that both first- and second-order rules result in harvesting decisions that produce a stream of discounted profits within 1% of the maximum.

* The approximate optimality of the $E(X)$ curve as employed in Fig. 2 can be derived from the first-order conditions in the Appendix. Suppose that the optimal approach from some stock level X_t involves values for the Lagrange multipliers of $\lambda_t = \lambda + \varepsilon_t$ and $\lambda_{t+1} = \lambda + \varepsilon_{t+1}$, where λ is the value of the multiplier at the certainty-equivalence equilibrium. Then the first and second of the first-order conditions can be shown to imply:

$$\frac{(pF_X - c)[\delta + M + (1 - M)F_X]}{(1 - M)F_X} = pF_X + \varepsilon_{t+1} + \varepsilon_t.$$

If the sum of ε_{t+1} and ε_t is small (which seems especially likely if convergence is oscillatory), then the above equation will be closely approximated by equation (4) in the text, and hopefully not too far from the solution to the underlying stochastic optimization problem.

It is difficult to make such comparisons in the whiting fishery. Without a joint distribution for recruitment and other bioeconomic parameters we do not have the necessary ingredients for the appropriate stochastic problem. As we will see in the next section, many of the estimates for equilibrium stock are around 1.0 million metric tons. This is within 30% of the 1989 estimate of 1.3 million metric tons for mean annual biomass (Dorn and Methot, 1989; Table 12). It would appear, at least superficially, that the approximately-optimal decision procedure described above can be appropriately applied to the Pacific whiting fishery.

3. Calibration of the Model for the Pacific Whiting Fishery. In the general model of the preceding section the production function, $Y_t = F(X_t, E_t)$, took on central importance in defining the stochastic equilibrium and the adaptive-management rule. When one attempts to specify and estimate such a function, one encounters at least two problems. First, where does one obtain a time series of estimates for average annual biomass, and second, how should one define effort?

In calibrating the model to the Pacific whiting fishery the author was fortunate to have estimates of average annual biomass from a stock-synthesis model developed by Dorn and Methot (1989). This time series seemed the best available and would also allow a comparison of yield levels from two otherwise disparate modeling perspectives.

The definition of effort has always proven difficult. Ideally, one would like as precise a measure as possible of the actual volume of water "strained" per unit time. The closest practical measure might be the number of hours that a vessel had net in the water fishing. In a bioeconomic model, the analyst is further removed from the ideal measure because of the need to estimate the unit cost of effort. The measure adopted here is the number of vessels in the fishery. This measure is open to criticism because it may not correspond to the volume of water strained during a season, but it is a measure for which we have some data on unit annual cost.

Table 1 contains data on catch by U.S. vessels, estimates of mean annual biomass, and the number of vessels in the U.S. whiting fleet from 1981 to 1989. From 1985 onward the fleet has increased, with a jump from 42 vessels in 1988 to 65 in 1989. The estimate of mean annual biomass has declined from 2.225 million metric tons in 1986 to 1.315 million metric tons in 1989. Dorn and Methot believe that this reflects the "mining" of the strong 1980 and 1984 year classes that were recruited into the fishery in 1982 and 1986, respectively. (Note the jump in average annual biomass in those years.)

Table 2 contains the regression results when the data in Table 1 were used to estimate Cobb-Douglas and exponential production functions. The Cobb-Douglas function takes the form $Y = qX^\alpha E^\beta$, and is linear logs. It contains, as a

Table 1. Data on catch, mean annual biomass and effort in the U.S. Pacific whiting fishery

Year (t)	Catch (Y_t)*	Biomass (X_t)†	Effort (E_t)‡
1981	44 395	1 384 000	21
1982	68 488	2 000 000	17
1983	73 150	1 805 000	19
1984	81 610	1 742 000	21
1985	35 586	1 685 000	17
1986	85 103	2 225 000	25
1987	110 792	2 012 000	31
1988	142 657	1 688 000	42
1989	204 038	1 315 000	65

*U.S. catch is measured in metric tons and is the sum of joint-venture and domestic catch from Table 1 of Dorn and Methot (1989).

†Biomass is measured in metric tons and is the mean annual estimate of biomass from Table 12 of Dorn and Methot (1989).

‡Effort is measured as the number of vessels in the U.S. Pacific whiting fleet as listed in the fax from D. E. Squires, NMFS, Southwest Fisheries Center, La Jolla, California, 18 June 1990.

special case, the standard catch-per-unit-effort production form (when $\alpha = \beta = 1$).

The exponential function takes the form $Y = X(1 - e^{-\alpha E})$. With this form it is impossible to catch more than current biomass, a logical characteristic, unfortunately not exhibited by the Cobb–Douglas production function. (Note: With the Cobb–Douglas form, as effort goes to infinity, so does catch.)

The exponential function may be estimated by regressing the natural log of the fraction of surviving biomass on effort. Ideally one would like to obtain an intercept not significantly different from zero and a significantly negative coefficient on effort. Alternatively, one can force the regression through the origin by suppressing the intercept.

The regression results for Cobb–Douglas and exponential production functions are given in Table 2. For the Cobb–Douglas form the coefficient for the natural log of q is not significantly different from zero, implying that q is not significantly different from one. The estimates of α and β are significant at the 5% level for a one-tail test. The adjusted R^2 is 0.8369. The Durbin–Watson statistic would appear to be in the inclusive range. The small sample size, however, makes determination of autocorrelation difficult.

In the least squares regression for the exponential function, the estimates of both the constant and the effort coefficient were significant. The adjusted R^2 was 0.9568. Because the Durbin–Watson seemed at the lower end of the inconclusive range the regression was run correcting first for first-order autocorrelation, then for second-order autocorrelation. Neither $AR(1)$ nor

Table 2. Regression results for the Cobb-Douglas and exponential production functions

A. Cobb-Douglas: $\ln Y_t = \ln q + \alpha \ln X_t + \beta \ln E_t + \varepsilon_t$				
Least squares				
Variable	Coefficient	Standard error	t-statistic	Two-tail significance
$\ln q$	-7.4226	7.4350	-0.9983	0.357
$\ln X$	1.0274	0.4979	2.0631	0.085
$\ln E$	1.2240	0.1878	6.5169	0.001
$R^2 = 0.8776$, Adjusted $R^2 = 0.8369$, $F = 21.5285$, $D - W = 1.4724$				
B. Exponential: $\ln(1 - Y_t/X_t) = \gamma + \alpha E_t + \varepsilon_t$				
Least squares				
Variable	Coefficient	Standard error	t-statistic	Two-tail significance
γ	0.0215	0.0068	3.1732	0.016
E	-0.0028	0.00021	-13.35	0.000
$R^2 = 0.9622$, Adjusted $R^2 = 0.9568$, $F = 178.232$, $D - W = 1.1146$				
Least squares, $AR(1)$				
Variable	Coefficient	Standard error	t-statistic	Two-tail significance
γ	0.0272	0.0187	1.4575	0.205
E	-0.0030	0.00043	-7.0358	0.001
$AR(1)$	0.5962	0.5030	1.1852	0.289
$R^2 = 0.9708$, Adjusted $R^2 = 0.9591$, $F = 83.209$, $D - W = 0.9544$				
Least squares, $AR(2)$				
Variable	Coefficient	Standard error	t-statistic	Two-tail significance
γ	0.0225	0.0121	1.8498	0.138
E	-0.0028	0.00036	-7.7592	0.001
$AR(2)$	-0.0783	0.6942	-0.1128	0.916
$R^2 = 0.9651$, Adjusted $R^2 = 0.9477$, $F = 55.368$, $D - W = 0.9676$				

$AR(2)$ were significant and in fact the Durbin-Watson statistics became smaller. The constant term became insignificant in both the $AR(1)$ and $AR(2)$ regressions but the estimate of α was essentially unchanged and remained significant.

The exponential form, with $\alpha > 0$ implies that production is strictly concave in effort, while the Cobb-Douglas function with $\beta > 1$ is not concave and would cause the stochastic equilibrium to be locally unstable. For this reason, and others noted above, we adopt the exponential form and run sensitivity analysis on α over the interval $[2.0E-2, 3.0E-2]$.

In an analysis of the tax returns of 13 vessels participating in the whiting fishery in 1988, Squires (1990) estimates annual variable costs per vessel to be approximately \$150 000. More difficult to estimate is the portion of fixed costs that should also be included when estimating annual operating costs. Squires calculates annual fixed costs by adding the costs of insurance, rent, association

dues, professional services and 7% of vessel acquisition costs (for vessels bought in 1978–1986, inclusive), for a total of approximately \$237 000 in 1988. The sum of annual variable and fixed cost payments comes to \$387 000.

It is difficult to argue that all the costs filed (*ex post*) on a tax form are relevant when a fisherman chooses to fish whiting, as opposed to some other species. One also suspects that there is an incentive to report as high a cost as possible (to reduce taxable income). In the numerical analysis of the next section we restrict our estimate of c to the interval (\$200 000, \$300 000).

Francis (1983), in fitting a cohort model to survey data, concluded that annual mortality was likely to be age-dependent, with rates varying from 0.195 for 5-year-old fish, to 0.757 for 11-year-old fish. Dorn and Methot use a constant rate of 0.20 for all cohorts. An average annual mortality rate of 0.25 is used in the Base-Case, with values of $M=0.20$ and $M=0.30$ also examined.

The price per metric ton for whiting has fallen since the early 1980s, when it peaked at slightly over \$151 in 1982. From 1986 to 1989 the price has been relatively stable between \$106 and \$110 per metric ton. Stochastic equilibria and adaptive management are examined for prices of \$100, \$110 and \$120 per metric ton.

Modeling by Dorn and Methot also provided estimates of recruitment, measured as billions of age two fish entering the fishery. They construct a time series from 1958 to 1988. There is a large range, from a low of 0.017 in 1987 to a high of 5.16 in 1963. The average over this 31-year period was 0.991 billion fish. An average 2-year-old whiting will weigh about 250 grams, transforming the 0.991 billion fish into an average recruitment of approximately 250 000 metric tons per year.

Though imprecise, we set $R=250\,000$ metric tons in the Base-Case parameter set. It is important to emphasize that while recruitment is highly variable, mean annual biomass is much less variable. Adaptive management does not depend directly on recruitment, only on an estimate of mean annual biomass. This has ranged from a high of 3.695 million metric tons in 1965, to low of 1.315 in 1989; with most year to year changes being less than 15%.

The final parameter required for both stochastic equilibrium and adaptive management is an estimate of the real (inflation-free) rate of discount. There has been a long standing debate among economists as to the appropriate rate of discount to employ when evaluating public investments or managing publicly held resources. There appears to be no simple answer. It depends on where the funds are coming from (whether they are displacing private investment or consumption) and whether the beneficiaries of the project derive a significant portion of their income from the investment or resource.

The question is perhaps more easily answered when managing a fishery resource. If there are a large group of fishermen, or if the species being managed constitutes only a small portion of the total income derived from fishing, then

the discount rate should be risk-free as well. Discount rates of 2, 4 and 6% will be evaluated.

4. Results. Restricting our analysis to the exponential production function, $Y = X(1 - e^{-\alpha E})$, we note that $F_X = (1 - e^{-\alpha E})$, and that $F_E = \alpha X e^{-\alpha E}$. Substitution into equation (4) results in:

$$\frac{c(1-M)(1-e^{-\alpha E})}{(p\alpha X e^{-\alpha E} - c)} = \delta + M. \quad (6)$$

Equation (5) takes the form:

$$R = MX + (1-M)X(1 - e^{-\alpha E}). \quad (7)$$

It is possible to solve equation (6) for an explicit expression for E , yielding:

$$E = -\ln \left[\frac{c(1+\delta)}{[p\alpha(\delta+M)X + c(1-M)]} \right] / \alpha. \quad (8)$$

This is our $E=E(X)$ curve in Figs 1 and 2. It will be used in the adaptive-management program.

Using equation (7) it is possible to eliminate E from equation (6) and obtain a quadratic expression in X . The positive root gives an expression for the optimal (stochastic) equilibrium stock. This expression is tedious to derive but some careful algebra should reveal:

$$X_R = (-B + \sqrt{B^2 - 4N})/2 \quad (9)$$

where:

$$B = -\frac{[p\alpha R(\delta+M) + c(1-M)\delta]}{[p\alpha(\delta+M)]} \quad (10)$$

and

$$N = -\frac{c(1-M)R}{[p\alpha(\delta+M)]}. \quad (11)$$

With X_R we can calculate long-run optimal effort as:

$$E_R = -\ln \{ (X_R - R) / [(1-M)X_R] \} / \alpha. \quad (12)$$

From the production function we know $Y_R = X_R(1 - e^{-\alpha E_R})$.

In the program in Table 3 we define and read the parameters α , c , δ , M , p and R and then calculate the stochastic equilibrium X_R , E_R and Y_R . You are then

asked if you would like to adaptively manage. If you answer yes, you are asked for an estimate of current-year biomass. Using this as the value of X in equation (8), and the same bioeconomic parameters as specified in line 10, the program calculates the approximately-optimal E (lines 140–150), then catch (line 160), and finally prints the results.

Table 3. A listing of the BASIC program to calculate the stochastic equilibrium and to adaptively manage based on estimates of current biomass

```

10 DATA 0.25E-2,2.250000,0.04,0.25,110,250000
20 READ A,C,D,M,P,R
30 B = -(P*A*R*(D+M) + C*(1-M)*D)/(P*A*(D+M))
40 N = -C*(1-M)*R/(P*A*(D+M))
50 XR = (-B + SQR(B^2 - 4*N))/2
60 ER = -LOG((XR - R)/((1-M)*XR))/A
70 YR = XR*(1 - EXP(-A*ER))
80 PRINT:PRINT "Long-Run Average Biomass=";XR
90 PRINT:PRINT "Long-Run Average Effort=";ER
100 PRINT:PRINT "Long-Run Average Catch=";YR
110 PRINT:INPUT "Do you want to Adaptively Manage? Yes = 1, No = 0.";W
120 IF W=0 GOTO 200
130 PRINT:INPUT "Current Biomass=";X
140 NUM = C*(1+D);DEN = P*A*(D+M)*X + C*(1-M)
150 E = -LOG(NUM/DEN)/A
160 Y = X*(1 - EXP(-A*E))
170 PRINT:PRINT "Current Biomass=";X
180 PRINT:PRINT "Recommended Effort=";E
190 PRINT:PRINT "Recommended Catch=";Y
200 END

```

The Base-Case parameter set is $\alpha = 0.25E-2$, $c = \$250\,000$, $\delta = 0.04$, $M = 0.25$, $p = \$110$ and $R = 250\,000$. Table 4 reports the calculated values for stochastic equilibrium and the approximately-optimal values for effort and allowable catch when the current biomass is 1.0E6, 1.5E6 and 2.0E6 metric tons. Each parameter (with the exception of R) is varied above and below its Base-Case value to determine its effect on the stochastic equilibrium and the adaptively-managed levels of effort and allowable catch. The results are presented in the 10 subcases (B through K) also contained in Table 4. Increases in long-run expected recruitment, R , will increase the equilibrium levels for biomass, effort and yield, but given the imprecise estimate of this value and the previously noted fact that the stochastic equilibrium is "seldom experienced", we do not present these results.

For the Base-Case parameter set the stochastic equilibrium occurs at a mean annual biomass of 957 748 metric tons, supporting a fleet of six vessels

Table 4. Stochastic equilibria and adaptive management

A. Base-Case parameter set			
	$\alpha = 0.25E-2$	$c = \$250\,000$	$\delta = 0.04$
	$M = 0.25$	$p = \$110$	$R = 250\,000\text{ mt}$
	$X_R = 957\,748\text{ mt}$	$E_R = 6\text{ vessels}$	$Y_R = 14\,083\text{ mt}$
When	$X = 1.0E6$	$E = 11$	$Y = 27\,128$
	$X = 1.5E6$	$E = 67$	$Y = 230\,159$
	$X = 2.0E6$	$E = 115$	$Y = 501\,441$
B. $\alpha = 0.20E-2$			
No commercial fishery in the long run. Vessels not sufficiently productive.			
When	$X = 1.0E6$	No commercial fishery	Stock too low
	$X = 1.5E6$	$E = 43$	$Y = 122\,881$
	$X = 2.0E6$	$E = 96$	$Y = 349\,730$
C. $\alpha = 0.30E-2$			
	$X_R = 883\,051\text{ mt}$	$E_R = 15\text{ vessels}$	$Y_R = 38\,983\text{ mt}$
When	$X = 1.0E6$	$E = 28$	$Y = 81\,921$
	$X = 1.5E6$	$E = 81$	$Y = 321\,930$
	$X = 2.0E6$	$E = 126$	$Y = 627\,606$
D. $c = \$200\,000$			
	$X_R = 867\,361\text{ mt}$	$E_R = 21\text{ vessels}$	$Y_R = 44\,213\text{ mt}$
When	$X = 1.0E6$	$E = 40$	$Y = 94\,668$
	$X = 1.5E6$	$E = 104$	$Y = 342\,837$
	$X = 2.0E6$	$E = 159$	$Y = 655\,897$
E. $c = \$300\,000$			
No commercial fishery in the long run. Fishing too costly.			
When	$X = 1.0E6$	No commercial fishery	Stock too low
	$X = 1.5E6$	$E = 40$	$Y = 142\,002$
	$X = 2.0E6$	$E = 84$	$Y = 377\,113$
F. $\delta = 0.02$			
	$X_R = 958\,887\text{ mt}$	$E_R = 6\text{ vessels}$	$Y_R = 13\,704\text{ mt}$
When	$X = 1.0E6$	$E = 10$	$Y = 25\,788$
	$X = 1.5E6$	$E = 64$	$Y = 220\,201$
	$X = 2.0E6$	$E = 110$	$Y = 482\,143$
G. $\delta = 0.06$			
	$X_R = 956\,702\text{ mt}$	$E_R = 6\text{ vessels}$	$Y_R = 14\,432\text{ mt}$
When	$X = 1.0E6$	$E = 12$	$Y = 28\,414$
	$X = 1.5E6$	$E = 70$	$Y = 239\,956$
	$X = 2.0E6$	$E = 120$	$Y = 519\,553$

Table 4—continued

H. $M=0.20$			
$X_R = 1\,075\,564$ mt		$E_R = 17$ vessels	$Y_R = 43\,609$ mt
When	$X = 1.0E6$	$E = 9$	$Y = 22\,556$
	$X = 1.5E6$	$E = 56$	$Y = 195\,652$
	$X = 2.0E6$	$E = 98$	$Y = 433\,735$
I. $M=0.30$			
No commercial fishery in the long run. Natural mortality too high.			
When	$X = 1.0E6$	$E = 13$	$Y = 31\,657$
	$X = 1.5E6$	$E = 77$	$Y = 262\,887$
	$X = 2.0E6$	$E = 132$	$Y = 563\,536$
J. $p = \$100\text{ mt}^{-1}$			
No commercial fishery in long run. Price too low.			
When	$X = 1.0E6$	$E = 0$	$Y = 0$
	$X = 1.5E6$	$E = 52$	$Y = 183\,544$
	$X = 2.0E6$	$E = 98$	$Y = 436\,090$
K. $p = \$120\text{ mt}^{-1}$			
$X_R = 921\,131$ mt		$E_R = 12$ vessels	$Y_R = 26\,289$ mt
When	$X = 1.0E6$	$E = 22$	$Y = 52\,823$
	$X = 1.5E6$	$E = 81$	$Y = 273\,585$
	$X = 2.0E6$	$E = 132$	$Y = 561\,549$

Vessel numbers are rounded to nearest whole vessel. Catch is rounded to nearest whole metric ton. Catch is calculated before rounding effort. Thus, fractional effort less than 0.5 vessels may give rise to slightly different catch for same biomass (Subcase H to J when $X = 2.0E6$).

harvesting 14 083 metric tons per year. These values are significantly below those observed in the previous decade (see Table 1).

When the current biomass increases from 1.0 to 2.0 million metric tons the adaptive rule recommends that fleet size increase from 11 to 115 vessels and that catch be allowed to increase from 27 128 to 501 441 metric tons. When current biomass is 1.5 million metric tons, a recommended fleet of 67 vessels would harvest 230 159 metric tons. These latter values are very similar to the "observed" values for catch, biomass and effort in 1989 from Table 1.

From this single piece of analysis we might hazard a characterization of the whiting fishery. It is a fishery that will be strongly influenced by current bioeconomic conditions. It should be managed opportunistically. When stochastic recruitment "deals a full house", maximization of expected present value says the fleet should significantly expand to harvest the windfall. The downside, of course, is that when recruitment deals nothing, the fleet must "fold 'em" and walk. To quote the Kenny Rogers song, fisheries managers have to

"know when to hold 'em and know when to fold 'em". In the U.S. and elsewhere, unfortunately, managers and fishermen have been slow to walk, trying to stay in the game when bioeconomic conditions indicate one should leave (at least temporarily).

The program in Table 3 indicates when fishing would reduce present value by returning a negative value for effort and catch. This can occur in the long-run stochastic equilibrium or in the short-run under adaptive management. In fact, for a given set of bioeconomic parameters a fishery that is unprofitable in the long-run may continue to be fished if strong recruitment or favorable prices prevail. Conversely, a fishery which is profitable in the long-run (stochastic equilibrium) may be shut down in the short-run because biomass has declined below a level that would support positive effort and catch along the optimal approach path. Recall the interpretation of $X_{\pi=0}$ in Figs 1 and 2.

The first situation is shown in Subcase B where, when vessel productivity declines from $\alpha = 0.25\text{E-}2$ to $\alpha = 0.20\text{E-}2$, there is no fishing in the stochastic equilibrium. If a run of strong recruitment (or a temporary moratorium) pushes biomass up to $1.5\text{E}6$ metric tons a fleet of 43 would be allowed to harvest 122 881 metric tons. In Subcase C, where $\alpha = 0.30\text{E-}2$, the stochastic equilibrium has a biomass of 883 051 metric tons supporting 15 vessels and an annual yield of 38 983 metric tons. If recruitment pushes biomass up to $1.5\text{E}6$ metric tons, adaptive managers would send out 81 vessels to harvest 321 930 metric tons.

In Subcase E, with an annual vessel cost of \$300 000, there would be no fishing in the stochastic equilibrium. A biomass level of $1.0\text{E}6$ is still below $X_{\pi=0}$. At a biomass of $1.5\text{E}6$ a fleet of 40 vessels is allowed to harvest 142 002 metric tons.

The value for $X_{\pi=0}$ when $p = \$100$ is precisely $1.0\text{E}6$ metric tons (see Subcase J). The fishery is not profitable in the long run at this price, but short-run biomass levels of $1.5\text{E}6$ and $2.0\text{E}6$ would support fleets of 52 and 98 vessels.

A systematic analysis of the results in Table 4 will reveal:

- (i) an increase in α will reduce equilibrium biomass while increasing fleet size and catch (Subcase A to C);
- (ii) an increase in cost, c , will increase equilibrium biomass, reducing effort and catch (Subcase D to A);
- (iii) an increase in the discount rate has relatively little impact, reducing equilibrium biomass slightly, causing a fractional increase in effort and a slight increase in catch (Subcase F to G);
- (iv) an increase in natural mortality might shut down the fishery in the long run and has the effect (similar to an increase in the discount rate) of increasing effort and catch in the short run (before fish die of natural causes; see Subcase H to I), finally;

- (v) an increase in price may make the fishery tenable in the long run and will increase effort and yield when adaptively managed at the same level of biomass (Subcase J to K).

It is a bit difficult to compare the results of Table 4 to the results of Francis (1983), Swartzman *et al.* (1983, 1987) and Dorn and Methot (1989). All of the models are cohort models and none are bioeconomic, in the sense of maximizing a present value measure. Perhaps the only common denominator is average yield. This is difficult to calculate in anything but a naive way because the cohort models are frequently run with constant fishing mortality or with constraints that prevent the biomass from declining below some bound. With that caveat in mind, we note that a simple average of yields listed in the first row of Table 3 from Swartzman *et al.* (1983) is 193 666 metric tons. The average yield from Table 2 of Swartzman *et al.* (1987) is 184 000 metric tons. From Dorn and Methot (1989) we have previously noted that average yield ranges from 178 000 to 244 000 metric tons for low risk runs and from 205 000 to 251 000 metric tons for high risk runs. If one averages the 44 yields (including zero yield when the fishery is shut down in the long or short run) from Table 4 in this paper one obtains 195 552 metric tons. While the models are very different in their biological and economic details, from the perspective of average yield they would appear to be in the same ballpark.

5. Conclusions. The Pacific whiting has become an important commercial species for both the U.S. and Canada. Both countries participate in joint-venture fisheries, where domestic trawlers capture whiting and off-load onto foreign processing vessels. Several papers published in the 1980s have examined population dynamics within age-structured models. Recruitment is thought to be independent of spawning biomass, and has been treated as a random variable. Because older and larger fish migrate further north, the age-structure of the resource can influence the availability of fish in Canadian waters.

While these models have been rich in biological detail, they have not adequately incorporated the economic factors which affect the commercial value of the resource, nor have they tried to determine optimal fleet size. The biological detail present in these models necessitates numerical analysis, such as Monte Carlo simulation, to determine the properties of the model and to develop average yields that might be used in making recommendations for allowable catch.

In this paper we have traded-off the biological detail of a cohort model in order to incorporate some of the economic factors thought to be important in the Pacific whiting fishery. The simple bioeconomic model of Section 2 permitted us to: (1) pose a stochastic optimization problem that sought to

maximize the present value of expected net revenue; (2) solve the certainty-equivalent problem for the stochastic equilibrium and an approximately-optimal rule for adaptive management; and (3) portray the equilibrium (Fig. 1) and show how the adaptive-management rule would operate (Fig. 2).

Data on catch, mean annual biomass and vessel numbers allowed for the direct estimation of a fishery production function. Cobb–Douglas and an exponential function both gave reasonable fits. The exponential form makes more sense biologically, gave a slightly better fit and for the parameter estimate was strictly concave in effort. This form was used and a range of values for the other bioeconomic parameters was obtained from previous biological and economic research.

In the bioeconomic model, long-run (stochastic) equilibrium depended on the production parameter, annual vessel cost, the discount rate, natural mortality, exvessel price and long-run average recruitment. In the short-run, using the adaptive-management rule, fleet size and allowable catch depended on the first five parameters and current biomass (instead of recruitment). Recommendations for short-run fleet size and allowable catch could fluctuate widely depending on the bioeconomic parameters, especially current biomass. From the Base-Case parameter set we observed that a current biomass of 1.0E6 metric tons would commend a fleet of only 11 vessels harvesting 27 128 metric tons. If current biomass were 1.5E6 metric tons, 67 vessels could harvest 230 159 metric tons and, if biomass increased to 2.0E6 metric tons (perhaps in the vicinity of “pristine equilibrium”), 115 vessels could harvest a 501 441 metric tons.

Such results characterize what might be called an opportunistic fishery, requiring a flexible fleet of generalist vessels able to respond to windfall recruitment and to shift to other fisheries when bioeconomic conditions are no longer favorable. Such flexibility has not been present in the U.S. or Canadian fishing industry, where effort seems quick to expand, but slow to contract. Managers and the fishing industry need to explore ways of increasing flexibility.

To use the adaptive-management rule we need an estimate of current-year biomass. The cohort models, especially the stock-synthesis model of Dorn and Methot (1989), can provide such an estimate. The age-structured models also have the advantage of being able to project changes in the abundance of particular cohorts. Such information might be important in determining spawning potential and the availability of whiting in Canadian waters.

This model should not be viewed as a replacement or even as a competitor for the niche occupied by the more complex biological models within the current “management landscape”. Rather, it should be used to complement the analysis of such models in seeking the economically efficient and equitable distribution of the Pacific whiting resource.

APPENDIX

The Lagrangian for the certainty-equivalent problem has first-order conditions requiring:

$$\frac{\partial L}{\partial E_t} = \rho^t \{ pF_E - c - \rho \dot{z}_{t+1}(1-M)F_E \} = 0$$

$$\frac{\partial L}{\partial X_t} = \rho^t \{ pF_X + \rho \dot{z}_{t+1}(1-M)[1-F_X] \} - \rho^t \dot{z}_t = 0$$

$$\frac{\partial L}{\partial [\rho \dot{z}_{t+1}]} = \rho^t [(1-M)[X_t - F(X_t, E_t)] + R - X_{t+1}] = 0.$$

In steady state these conditions imply:

$$\rho \dot{z} = (pF_E - c) / [(1-M)F_E]$$

$$\rho \dot{z} [(1-M)[1-F_X] - (1+\delta)] = -pF_X$$

$$R = MX + (1-M)F(X, E).$$

The second steady state equation can be further simplified to:

$$-\rho \dot{z} [(\delta + M) + (1-M)F_X] = -pF_X.$$

Multiplying through by -1 and substituting the first steady-state expression for $\rho \dot{z}$ yields:

$$(pF_E - c) [(\delta + M) + (1-M)F_X] = pF_X [(1-M)F_E].$$

This last expression can be further simplified to:

$$\frac{c(1-M)F_X}{(pF_E - c)} = \delta + M$$

which is given as equation (4) in the text. Equation (5) in the text is the third of the steady-state equations listed above.

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Pre-exploitation Abundances of Important Large Recreational and Commercial Fishes off Southern California

University of California, San Diego
R/F-125
1988-1990
Project Initiated: October 1, 1988
Project Completed: January 31, 1990

Paul K. Dayton and Alec D. MacCall

Introduction

The goal of this Sea Grant project was to estimate pre-exploitation abundances for the white seabass (*Atractoscion nobilis*), the yellowtail (*Seriola lalandei*), and the giant sea bass (*Stereolepis gigas*). Baseline measures of abundance or biomass of fish and wildlife populations are valuable for assessment of human-induced changes in those populations. Such measures are, however, rare. Populations may be altered long before the need for baseline information is recognized.

Commercial fisheries for the white seabass, yellowtail, and giant sea bass were well established by the late 1910s and early 1920s, a period in which significant changes occurred in the populations of these three large predatory fishes (Figures 1-3). Fisheries data from this period to 1990 suggest that California populations of these fishes are in various states of depletion, but prefishery population levels have not been estimated.

A unique data set collected by the Avalon Tuna Club of Santa Catalina Island (Figure 4) contains information that predates large-scale commercial fishing off Southern California (Macrate, 1948). This data set contains records of the heaviest white seabass, yellowtail, and giant sea bass caught each year by a member of the club. To the extent that size composition reflects fishing pressure, these data provide a means of estimating pre-exploitation biomasses for white seabass and yellowtail populations by using a maximum likelihood approach. Estimates are made by combining a simple population model and a statistical model. Our original intent was to use the same modeling approach for the giant sea bass. However, inadequate data on the life history of this fish precluded use of

this maximum likelihood approach; a lower limit of its pre-exploitation biomass was estimated by using catch data only.

The General Model

Maximum likelihood estimates of the pre-exploitation abundances for the white seabass and the yellowtail were generated by combining (1) a harvested population model generating the distribution of yearly weight frequencies, (2) a statistical model for the probability distribution of the heaviest fish in a sample from the model population, and (3) annual observations of the heaviest fish caught by a member of the Avalon Tuna Club. The statistical model links the records of the Avalon Tuna Club to the distribution of weight frequencies in the modeled population, providing a basis for

estimating the likelihood that the Avalon Tuna Club data would have been observed, given the assumed population model.

The Population Model. The purpose of the population model is to provide distributions of annual weight frequency of an assumed resident, self-sustaining population in California waters. Components of the model include length-at-age and weight-at-length relationships, a stock-recruitment relationship (Figure 5), age of recruitment to the fishery, and the historical commercial and sport harvests. Fitted parameters from the population model are initial population size and instantaneous mortality rate.

By assuming a constant instantaneous natural mortality rate (M) and an initial population size (B_0), we constructed a stable age

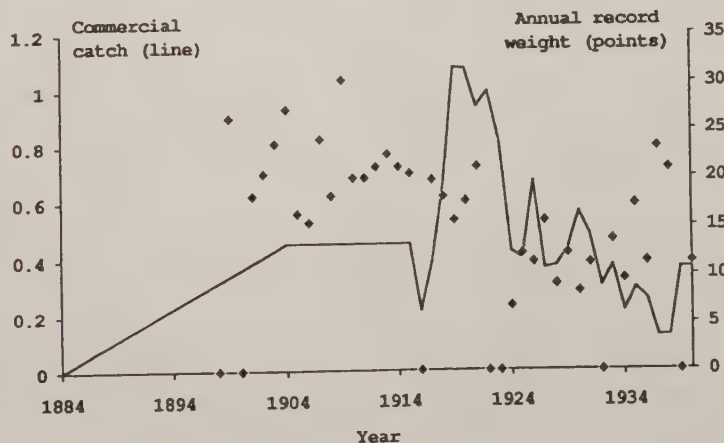


Figure 1. Commercial catch (1000 tons) and record weight (kg) of white seabass caught by a member of the Avalon Tuna Club, 1884-1940. Commercial catch for the period 1904 to 1915 set constant at 454 tons and linearly interpolated to that level beginning with zero catch in 1884 (Frey, 1971). See text for remaining data sources.

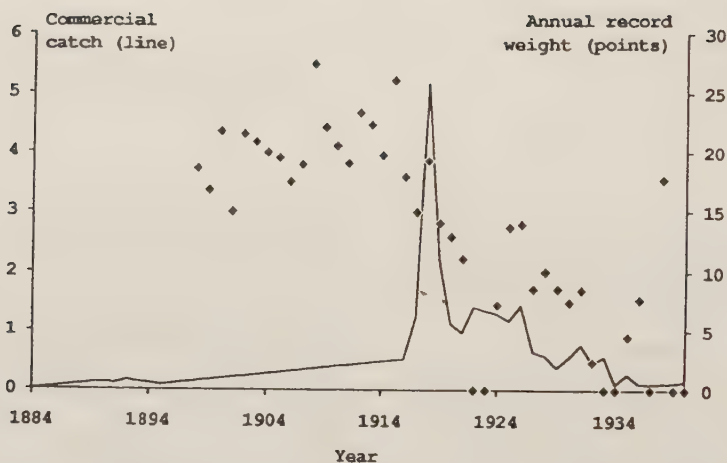


Figure 2. Commercial catch (1000 tons) and record weight (kg) of yellowtail caught by a member of the Avalon Tuna Club, 1884–1940.

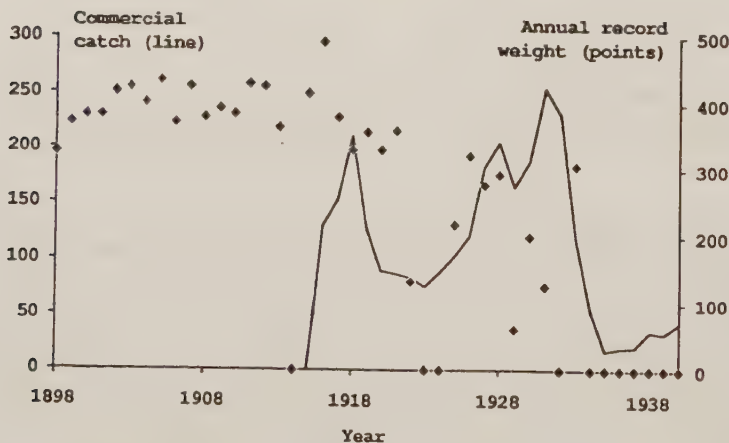


Figure 3. Commercial catch (1000 tons) and record weight (kg) of giant sea bass caught by a member of the Avalon Tuna Club, 1898–1940.

frequency distribution. Age-length (with variability) and length-weight relationships from the literature were used to convert the age frequency distribution to a weight frequency distribution, with fish summed over discrete weight categories of unit width. Constant recruitment to the model population in the absence of other extraneous perturbation leads

to a constant population abundance and weight frequency distribution over time.

Such constancy ceases under conditions of harvesting, and the weight distribution subsequently varies with the removal of portions of the model population according to historical commercial and sport catch records.

The population model runs from 1884 to 1940. Avalon Tuna Club records begin in 1898. The period from 1884 to 1897 is included to incorporate the effects of earlier years of commercial fishing for which records are available.

The Statistical Model. Based on a year-specific weight frequency distribution from the population model, the statistical model provides a method of determining a year-specific probability distribution for the heaviest fish in a sample from the population. This extreme-value probability distribution is taken from Hogg and Craig (1965):

$$f(W_{\max} | S) = S [F(W)]^{S-1} f(W), \quad (1)$$

where S , $f(W)$, and $F(W)$ are the sample size, weight frequency distribution, and cumulative weight frequency distribution, respectively, for the model population. Because the year-specific weight frequency and cumulative weight frequency distributions ($f(W)$ and $F(W)$, respectively) are functions of the population model and its estimated parameters, the resulting year-specific probability distribution for the heaviest fish taken in a sample from the population is also a function of those parameters. Although the Avalon Tuna Club records do not include sample size, and hence true sample size is unknown, the mean sample size can be assumed to be approximately proportional to the year-specific abundance in numbers of fish (N) given by the population model. The constant of proportionality (q , where $S_{\text{mean}} = qN$) is a parameter to be estimated. Because actual S varies about S_{mean} , and is a relatively small number, S is assumed to have a Poisson distribution. The density function used in the likelihood equation is the weighted mean of the $f(W_{\max} | S)$ values from equation (1), with weighting from the Poisson frequency distribution $p(s)$. Thus, if a maximum weight observation exists for a particular year,

$$f(W_{\max} | S_{\text{mean}}) = \sum_{s=1}^{\infty} [f(W_{\max} | s) p(s | S_{\text{mean}})], \quad (2a)$$

and if there is no observation,

$$f(\text{no obs}) = p(s = 0 | S_{\text{mean}}). \quad (2b)$$

Note that lack of a recorded maximum-sized fish for a particular year (which occurs in these time series) is likely to indicate that recreational catch rates, and hence available biomass, were low. The stochastic treatment allows this inference to be incorporated explicitly in the likelihood function.

By comparing the observed annual

records of the Avalon Tuna Club with the corresponding probability distribution for the heaviest fish, a year-specific probability can be determined for each year of the interval 1898 to 1940 in the model simulation. The sum of the natural logarithms of those year-specific probabilities over the period 1898 to 1940 is the log-likelihood function for the population model and its specific input.

The simplex algorithm (Nelder and

Mead, 1965) is combined with a single- and double-parameter searching method to locate the combination of parameters that leads to the maximum likelihood. Those parameters include the pre-exploitation abundance and the instantaneous mortality rate from the population model and the constant of proportionality for sample size from the statistical model.

Two methods of testing precision of the results were used. The first estimated minimum-variance bounds for the parameters by using second and mixed partial derivatives (Norden, 1972, 1973). The second method varied the assumptions of the population model, including the stock-recruitment function, the age of recruitment to the fishery, the biomass of seasonal migrants to the population and commercial fishery, the period of extensive sport fishing, the variability and density dependence of length-age functions, and the stability of the starting age distribution.

Results

White Seabass. Model simulations suggested that the pre-exploitation biomass of white seabass was near or slightly greater than 20,000 tons, with coefficients of variation on the order of 0.25 to 0.4. Corresponding population abundances ranged from approximately 2 million to 2.5 million fish. Results also suggested an instantaneous natural mortality rate on the order of 0.08 yr⁻¹ (coefficient of variation ~ 0.15), somewhat lower than previous estimates of 0.33 yr⁻¹ (Thomas, 1968) and 0.12 yr⁻¹ (MacCall, et al., 1976). Figure 6 shows the correspondence of model biomass to annual record weight of white seabass taken by the Avalon Tuna Club. Similarly, the correspondence of model biomass to annual commercial catch is shown in Figure 7.

Yellowtail. Estimates of pre-exploitation biomass and abundance for the yellowtail were similar to the estimates for the white seabass, that is, just greater than 20,000 tons and 2 million fish, respectively. However, the coefficients of variation for the

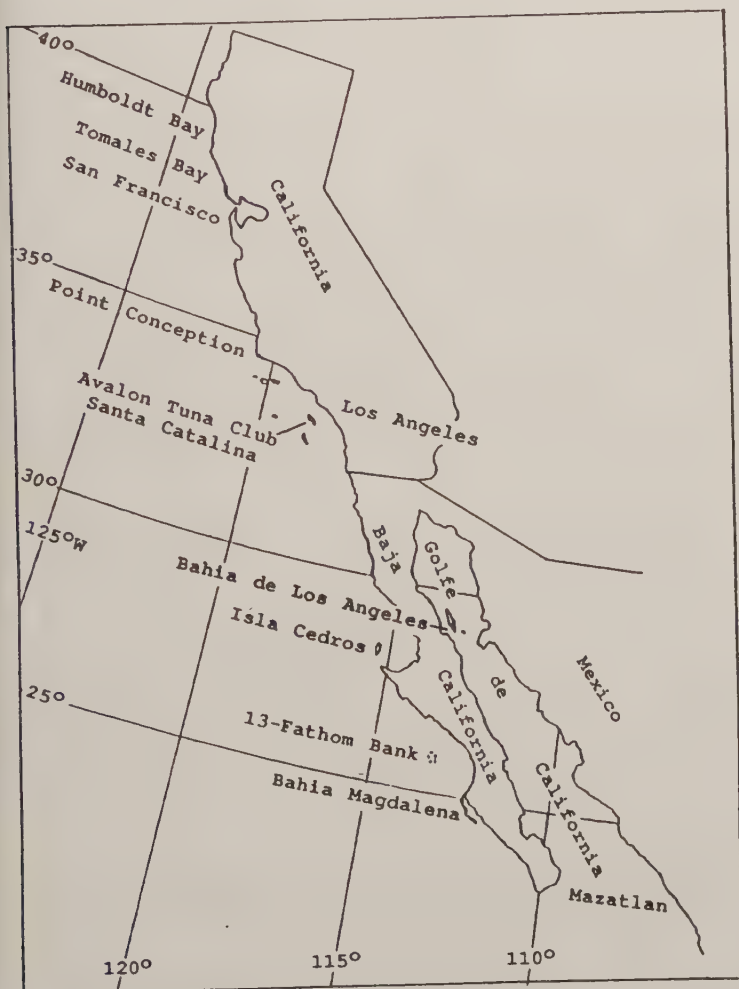


Figure 4. Oceanic area pertinent to study.

yellowtail were on the order of 0.05 to 0.12, and therefore were much smaller than is the case for the white seabass. Instantaneous natural mortality for the yellowtail was estimated to be about 0.09 yr^{-1} , slightly greater than that of the white seabass. The correspondence of model biomass to annual record weight of yellowtail taken by the Avalon Tuna Club is shown in Figure 8; Figure 9 shows the correspondence of model biomass to annual commercial catch.

Giant Sea Bass. As noted before, insufficient information on the life history of the giant sea bass, particularly age-length-weight relationships, precluded the estimation of pre-exploitation biomass for this fish with the model used here. However, Frey (1971) concluded that the combination of commercial fishing, slow recruitment, and continued sportfishing has inhibited the recovery of the giant sea bass. If this is the case, then the lower limit for that biomass can be approximated by summing the total commercial catch of giant sea bass during the period from 1916 (when records begin for the commercial fishery) to 1940. The sum of those landings is approximately 1300 tons. Certainly, this estimate could be improved if information on growth and mortality of the giant sea bass and estimates of the sportcatch during this period were available. Still, the sportcatch before 1940 probably was negligible relative to the commercial catch, and regardless of growth and mortality, recruitment is sufficiently low to prevent rapid turnover of the population.

Discussion

The essence of the maximum likelihood approach used here is the search of a multivariate response surface for its peak. In this model, the likelihood surface was a function of three parameters that were subject to at least one major constraint: The initial abundance and mortality rate must allow an initial population sufficiently large to withstand the removal of the biomass taken in the commercial catch. On the response surface, this constraint manifests itself in the form of a boundary

beyond which any solution is infeasible. Figure 10 illustrates likelihood response surfaces for the white seabass and the yellowtail when only mortality and initial abundance are varied. For both the white seabass and the yellowtail, the peak of the surface is located close to this boundary of feasible solutions, suggesting that these populations were fished to low levels during the early part of this century. The close

correspondence between the parameter estimates for the white seabass and the yellowtail suggests these two fishes were similar in population size and have similar life histories.

In general, results for the white seabass and the yellowtail were robust to the multiple assumptions required by this modeling approach. Furthermore, these results are the only available estimates of pre-

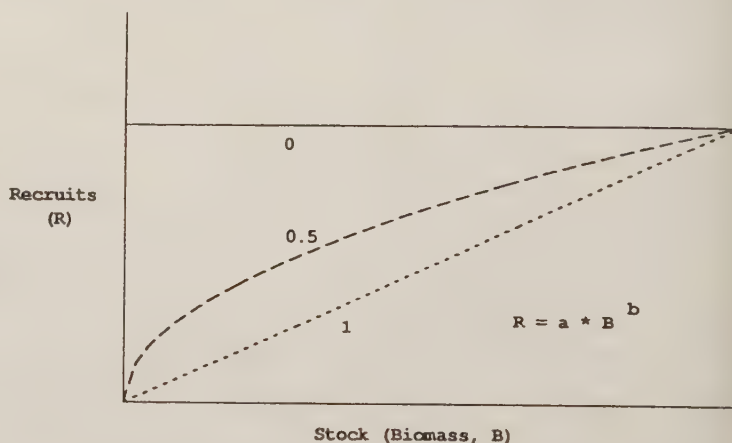


Figure 5. Stock-recruitment relationships used in the model. The three lines correspond to the indicated values of b .

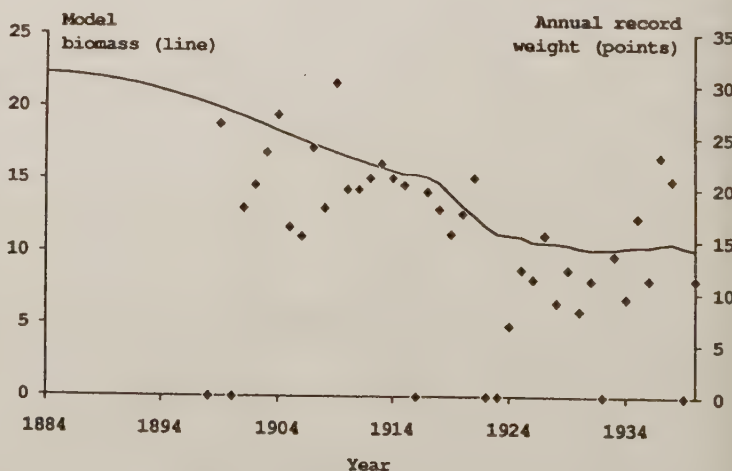


Figure 6. Model biomass (1000 tons) and annual record catch (kg) of white seabass by an Avalon Tuna Club member, 1884-1940.

exploitation abundance for the white seabass and yellowtail. As such, they provide the only indication of the severity of historical exploitation and the extent of recovery that would be necessary to return these populations to their natural state. Clearly, however, these estimates apply to the natural state in the late 1800s. To suggest that in the absence of exploitation these fish populations would be at similar levels

today requires the assumption that the overall influence of the pertinent demographic and environmental conditions has not changed. In the absence of information on such changes, the estimates generated here provide our best indication of the natural state of these fishes.

As such, this information should be useful as a guide for programs such as California's Ocean Resources Enhancement and Hatchery Program

(OREHP). One of the projects funded by OREHP has been development of a cost-benefit assessment model of hatchery performance and stock rehabilitation, with particular emphasis on the white seabass. As the population dynamics of the white seabass have heretofore not been well known, the OREHP investigation has necessarily relied on many assumptions about vital rates and related population properties. Although the white seabass is thought to be depleted, data have been insufficient to obtain clear results by using standard fishery assessment models (MacCall et al., 1976).

To the present, assessment and management of the white seabass, the yellowtail, and the giant sea bass have been based on the assumption that California's catches are taken from the seasonal northward migrants, which has largely been the case over most of the last half century. Managers have understandably hesitated to impose restrictions on harvests from a resource over which they would seem to have little real control. Management based on conservation of a strictly resident stock would require much greater restrictions on fishing effort. In addition, our results indicate natural mortality is low, which also suggests fishing mortality must be kept low if a resident stock is to be sustained. Presumably a population composed of both resident and migrant fish would allow intermediate levels of fishing. Until now, lack of sufficient information on the early resources and fisheries has prevented quantitative consideration of resident Southern California stocks of these species. The estimates provided by this study give managers a new view of the potential productivity of these stocks in Southern California. For example, the results allow application of the Gulland potential yield rule-of-thumb, $Y_{pot} = MB_0/2$, where Y_{pot} is potential yield. These cases indicate a Y_{pot} on the order of 500 to 900 metric tons. Indeed, the recent interest in artificial propagation of white seabass would seem to be more consistent with a management of a resident rather than a migrant resource. If artificial

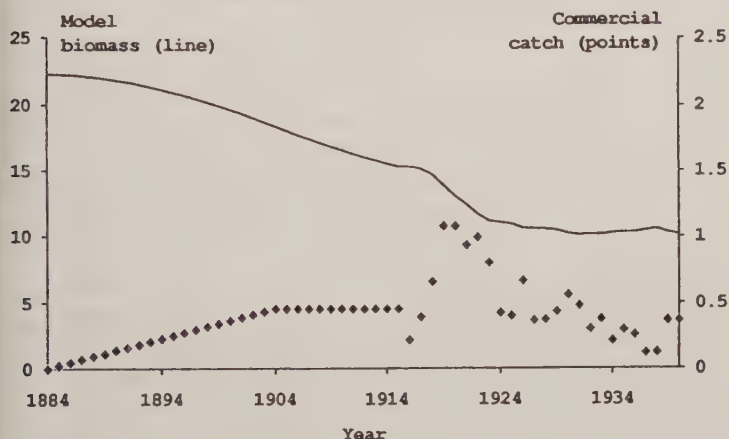


Figure 7. Model biomass and commercial catch of white seabass, 1884-1940. Both vertical axes are in units of 1000 tons.

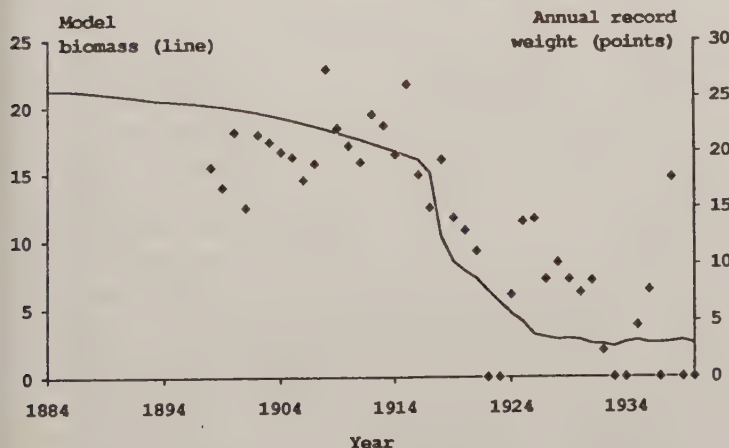


Figure 8. Model biomass (1000 tons) and annual record catch (kg) of yellowtail by an Avalon Tuna Club member, 1884-1940.

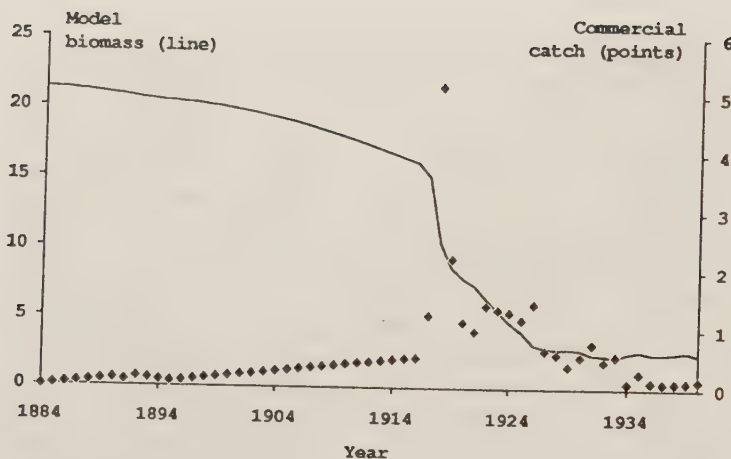


Figure 9. Model biomass and commercial catch of yellowtail, 1884–1940. Both vertical axes are in units of 1000 tons.

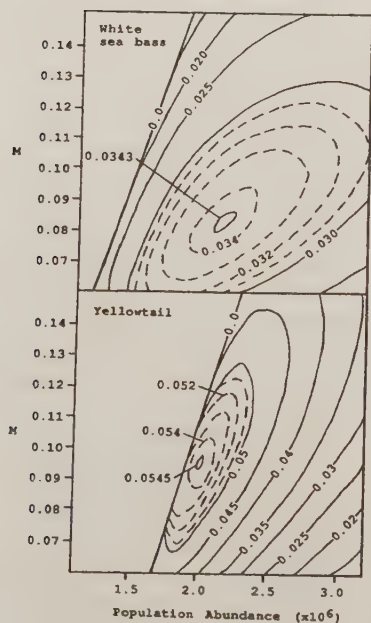


Figure 10. Contour plots of model response surfaces for the white seabass and the yellowtail. Isobars are of geometric mean probabilities, determined as antilog (log-likelihood/43 years).

propagation is to be attempted seriously, it is desirable and perhaps essential that management of these populations in Southern California be made consistent with conservation of a resident population. This study provides information which will help fishery scientists evaluate and managers decide whether the benefits of resident-based population management are worth the restrictions that would have to be imposed on fisheries.

Cooperating Organizations

Avalon Tuna Club, Avalon, California
California Department of Fish and Game,
Long Beach, California
National Marine Fisheries Service,
Southwest Fisheries Center, La Jolla,
California
University of California, San Diego
Supercomputer Center

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Lectures

- MacCall, A. D. Historical changes in the California Current ecosystem. Seminar presentation. NOAA/NMFS Tiburon Laboratories, Tiburon, California, March 1990.
- MacCall, A. D. Historical changes in the California Current ecosystem. Seminar presentation. University of California Bodega Marine Laboratories, Bodega Bay, California, March 1990.
- MacCall, A. D. Historical changes in the California Current ecosystem. Seminar presentation. California State University, Hayward, California, May 1990.

STATUS OF DOLPHIN STOCKS IN THE EASTERN TROPICAL PACIFIC

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Abstract. Since the passage of the U. S. Marine Mammal Protection Act, approximately 1.25 million dolphins have been killed incidentally during purse seine fishing operations for yellowfin tuna (*Thunnus albacares*) in the eastern tropical Pacific Ocean. The three species of pelagic dolphins primarily involved in this fisheries interaction are the spotted dolphin (*Stenella attenuata*), spinner dolphin (*Stenella longirostris*), and common dolphin (*Delphinus delphis*). We review the status of these species relative to stock structure, current population size, levels of fishery-related mortality, and trends in abundance. Abundance estimates have been derived from two sources: data collected by observers on research vessels and data collected by observers on tuna vessels. Estimates of incidental mortality are currently derived only from data collected by observers on tuna vessels. There is no evidence of any significant change in abundance for any of these three species since 1985. However, declines in abundance have been detected over the last 15 yr.

INTRODUCTION

The National Marine Fisheries Service (NMFS) is responsible for assessing the status of dolphin stocks subject to incidental mortality by tuna purse seiners in the eastern tropical Pacific Ocean (ETP). Over 1.25 million dolphins are estimated to have been killed by this fishery since the passage of the U. S. Marine Mammal Protection Act (MMPA) in 1972 (Table 1). The major species affected are the spotted dolphin (*Stenella attenuata*), spinner dolphin (*S. longirostris*), and common dolphin (*Delphinus delphis*).

In 1984, the Service was mandated under the MMPA to commence a scientific research program to monitor trends in abundance of dolphin stocks that may be adversely affected by the purse seine fishery for yellowfin tuna (*Thunnus albacares*) in the ETP. Should declines in any stocks be detected, the Secretary of Commerce would be required to modify the applicable quotas as necessary to ensure that none of the stocks are disadvantaged. The NMFS dolphin monitoring program consists of three elements: (1) a series of seven research vessel surveys over eleven years (1986-1996) using dedicated research vessels; (2) analyses of marine mammal sightings data collected by observers aboard U. S. and non-U. S. tuna vessels; and (3) analyses of life history data collected by observers aboard U. S. tuna vessels. The research vessel surveys were designed

TABLE 1. Number of eastern tropical Pacific dolphins estimated to have been killed in commercial tuna purse seine fishing operations from 1973 through 1990. Data from Smith (1979, 1983), Wahlen (1986), and Punsley (1983) for the years 1973-1978, Inter-American Tropical Tuna Commission (1989, 1991, 1992) for the years 1979-1990, in addition to Hall and Boyer (1990, 1992) for the years 1989-1990. Abbreviations are as follows: NSpot (northern offshore spotted dolphin), SSpot (southern offshore spotted dolphin), ESpin (eastern spinner dolphin), WSpin (whitebelly spinner dolphin), NCom (northern common dolphin), CCom (central common dolphin), and SCom (southern common dolphin).

Year	NSpot	SSpot	ESpin	WSpin	NCom	CCom	SCom
1973	74 448	10 152	18 400	30 800	5100	5100	0
1974	76 900	0	17 800	25 900	4300	4500	0
1975	75 068	1532	17 100	26 200	5000	5000	0
1976	50 183	24 717	14 700	29 400	4000	4000	0
1977	18 522	378	1800	4900	2000	2000	0
1978	12 825	675	1100	3400	1100	1100	0
1979	8870	2348	1460	1312	4161	2342	94
1980	13 058	6828	1108	8132	1060	963	188
1981	16 324	6376	2261	6412	2629	372	348
1982	15 427	4504	2606	3716	989	487	28
1983	3414	3608	745	4337	845	191	0
1984	15 940	4042	6033	7132	0	7403	6
1985	31 309	2786	8853	6979	0	6839	304
1986	67 989	5125	19 526	11 042	13 289	10 884	134
1987	51 685	3285	10 358	6026	8216	9659	6759
1988	36 137	2192	18 793	3545	4829	7128	4219
1989	52 093	3863	15 245	8302	1066	12 711	576
1990	32 267	1584	5378	6952	704	4053	272
Total	652 459	83 995	163 266	194 487	59 288	84 729	12 928

specifically to detect an annual change of approximately 10% per year for the northern offshore stock of spotted dolphin, and were not designed to estimate absolute abundance per se. The analysis of sightings data collected by observers on tuna vessels is being done cooperatively with the Inter-American Tropical Tuna Commission (IATTC), with the IATTC taking the lead on this research. The results of the studies will be included in a report to Congress in 1992. The purpose of this report is to provide a preliminary summary of findings to date. Any conclusions from this report should likewise be considered preliminary.

SPOTTED DOLPHIN

Distribution and stock structure

Three stocks of spotted dolphins are currently recognized: northern offshore, southern offshore, and coastal (Anonymous 1987). Perrin et al. (1985) recommended that schools of spotted dolphins should not be identified as coastal or offshore on the basis of geographic location alone. In addition they recommended that the division of northern and southern stocks be retained. Recent information on seasonal movement patterns (Reilly 1990) and patterns of morphological variation (Perrin et al. 1985) suggests that spotted dolphins move between the western and southern portions of their range. NMFS is currently evaluating the existing definitions of stock structure in spotted dolphins.

Population estimates

Holt and Powers (1982) estimated the absolute abundance of spotted dolphins in 1979 using data from research vessels alone (RVD) and from research and tuna vessel data combined (RVTVD). A preferred approach was not identified by Holt and Powers (1982); therefore, both estimates are given (Table 2). Seventy to 80% of the spotted dolphins were from the northern stock. The coastal stock estimates were 189 000 (RVD) and 114 400 (RVTVD). The coefficient of variation (CV) for these estimates varied between 20 and 30%.

Based on the first four research vessel surveys under the Congressionally mandated program to monitor changes in the abundance of ETP dolphins (1986-1989; Table 3), hereafter referred to as the Monitoring of Porpoise Stocks survey (MOPS) estimates, the population size of the northern stock of offshore spotted dolphin varied between 1 212 800 and 2 838 300, and averaged 1 992 750 (Sexton et al. 1992, Gerrodette and Wade 1992). The population estimate for the southern stock varied between 314 000 in 1986 to 721 400 in 1989, with an average of 508 525. The CV for all stocks ranged between 16 and 19%.

The objective of the MOPS surveys was to monitor trends in relative abundance. That is, Sexton et al. (1992) and Gerrodette and Wade (1992) attempted to minimize the

TABLE 2. Absolute abundance estimates of eastern tropical Pacific dolphins from research vessel data (RVD) and tuna vessel-research vessel data (TVRVD) for 1979 (Smith 1979).

	Northern spotted	Southern spotted	Eastern spinner	Whitebelly spinner	Common (pooled)
RVD 1979	1 682 000	584 600	292 900	570 200	921 000
RVTVD 1979	2 775 000	465 500	292 700	607 000	1 373 100

variance of the population estimates, while holding potential sources of bias constant from year to year. For example, in estimating stock abundance, Sexton et al. (1992) and Gerrodette and Wade (1992) assumed that the number of animals in each stock was a constant (over time) proportion of the area occupied by that stock and, therefore, sighting data from different strata could be pooled. This has the effect of reducing the variance of the population estimate, but increasing the potential for the estimates to be biased (see discussion in Sexton et al. 1992). Furthermore, no information on the probability of detecting a school of dolphins on the track line or the response of dolphins to the survey vessel (i.e., possible avoidance or approach) was available. Therefore, using the relative abundance estimates reported by Sexton et al. (1992) or Gerrodette and Wade (1992) as estimates of absolute abundance requires the assumption that all dolphin schools on the trackline were detected and that dolphins did not respond to the survey vessel.

Wade and Gerrodette (1992) reanalyzed the data from the first 5 yr (1986-1990) of the MOPS surveys using a different statistical analysis. By not pooling sightings data over all species and strata their analysis produced less precise but, presumably less biased estimates of relative abundance (Table 4). From this analysis, the estimated population size for the northern stock of offshore spotted dolphin for 1986-1990 varied between 658 300 and 2 205 500 with CVs between 26 and 36%. An average abundance estimate for the northern stock using this method is approximately 1 514 800. Estimates for the southern stock were between 85 800 and 475 800 with CVs between 48 and 86% with a mean of 267 400 animals.

In addition to the MOPS estimates, estimates of relative abundance have been produced for the northern and southern stocks (Table 5) based on sightings data from observers aboard tuna vessels (Anganuzzi and Buckland 1989, Anganuzzi et al. 1992a,b). For the northern stock, the abundance estimates (1986-1990) ranged from 2 553 000 to 3 165 000. The average estimate for the northern stock was 2 854 000. For the southern stock, the estimates were between 79 000 and 785 000, and averaged 394 500 (no estimate for the southern stock was reported for 1987). Because tuna vessels search nonrandomly, and tend to concentrate in areas of high dolphin abundance, these relative abundance indices may be positively biased if treated as estimates of absolute abundance.

Mortality estimates and mortality rates

Estimates of incidental mortality of dolphins in the tuna fishery show considerable mortality in the 1960s, with reductions thereafter due to regulations (Smith 1983, Table 1). Quotas of incidental mortality for U. S. fishermen were set for the northern offshore, southern offshore, and coastal stocks (20 500, 5697, and 250, respectively) in 1987 (Anonymous 1987). It should be noted that incidental mortality estimates (hereafter referred to as mortality estimates) for the coastal stock are considered unreliable because of the difficulty in separating the offshore and coastal stocks and because of the low level of observed fishing effort in nearshore waters. Also, estimates of mortality between 1959 and 1972 are considered very imprecise because of the small number of observed trips during this time period, uncertainty as to whether backdown procedures were used, and changes in the fleet towards larger vessels and therefore, are not included in this report (Lo and Smith 1986).

TABLE 3. Relative abundance estimates of eastern tropical Pacific dolphins from monitoring of porpoise stocks survey data (Sexton et al. 1992, Gerrodette and Wade 1992).

	Northern spotted	Southern spotted	Eastern spinner	Whitebelly spinner	Northern common	Central common	Southern common	Common (pooled)
1986	1 212 800	314 000	715 900	657 200	284 700	1 093 000	429 300	1 810 000
1987	1 901 700	486 800	707 200	750 400	163 200	619 600	243 500	1 026 300
1988	2 018 200	511 900	901 800	820 700	836 900	3 177 400	1 248 700	5 263 000
1989	2 838 300	721 400	1 200 000	1 170 100	411 200	1 561 100	613 500	2 585 700
MEAN	1 992 750	508 525	881 225	849 600	424 000	1 612 750	633 750	2 671 250

TABLE 4. Relative abundance estimates from monitoring of porpoise stocks survey data (Wade and Gerrodette 1992).

Year	Northern spotted	Southern spotted	Eastern spinner	Whitebelly spinner	Northern common	Central common	Southern common	Common (pooled)
1986	1 134 200	236 000	603 700	706 100	390 000	306 700	2 217 300	2 913 500
1987	1 582 600	475 800	444 700	1 220 700	23 500	348 100	152 000	523 600
1988	2 205 500	85 800	754 200	1 398 400	1 272 400	1 487 600	2 896 500	5 656 500
1989	1 993 600	451 900	748 800	1 280 000	473 600	261 000	3 664 000	4 398 600
1990	658 300	87 700	391 200	363 300	177 700	568 000	1 657 500	2 403 200
MEAN	1 514 840	267 440	588 520	993 700	467 440	594 280	2 117 460	3 179 080

TABLE 5. Relative abundance estimates from tuna vessel observer data (Anganuzzi and Buckland 1989, Anganuzzi et al. 1992a,b).

Year	Northern spotted	Southern spotted	Eastern spinner	Whitebelly spinner	Common (pooled)
1986	3 165 000	154 000	584 000	451 000	644 000
1987	2 953 000	-	384 000	650 000	364 000
1988	2 689 000	79 000	717 000	572 000	817 000
1989	2 910 000	560 000	389 000	705 000	547 000
1990	2 553 000	785 000	376 000	675 000	507 000
MEAN	2 854 000	394 500	490 000	610 600	575 800

Since 1986, increased observer coverage of U. S. and international fleets has yielded much more reliable estimates of mortality. The average estimated annual mortality between 1986 and 1990 for the northern stock was 48 040 animals, while the average for the southern stock was 3220. Furthermore, since 1986, estimated mortality of northern offshore spotted dolphins has declined, on average, by 7104 animals per year (linear regression of mortality versus years, $P=0.12$), and the southern stock by 650 animals per year ($P=0.16$).

Because of variability and bias in estimates of both population and incidental mortality, estimates of percent mortality can not be determined reliably. If the most recent estimates of relative abundance from the MOPS surveys are used to approximate absolute abundance, percent mortality can be estimated by dividing annual estimates of mortality by annual or average estimates of population abundance. Because trends in abundance were not detected between 1986 and 1990, the mean estimate for the years 1986-1990 from Wade and Gerrodette (1992) were used to estimate annual percent mortality (Table 6).

By this method, the northern offshore spotted dolphin had an average mortality rate of 3.2%, while the southern stock had an average mortality rate of 1.2% between 1986 and 1990. The mortality rates for northern offshore spotted dolphins have declined between 1986 and 1990 from 4.5 to 2.1%, while the southern offshore spotted dolphin mortality rates declined from 1.9 to 0.6%. It is likely that these estimates of percent mortality are positively biased, but the magnitude of the bias is unknown.

Assessment and status

Currently, the most reliable information on trends in abundance is based on sighting data collected aboard tuna vessels. At this time, too few data points (annual estimates) have been determined from the MOPS surveys to yield results with adequate statistical power. Using tuna vessel observer data, Anganuzzi and Buckland (1989)

TABLE 6. Percent dolphin mortality using average population estimates for the years 1986-1990 (Wade and Gerrodette 1992), and mortality estimates (Inter-American Tropical Tuna Commission [1989, 1991], and Hall and Boyer [1990, 1992]) for spotted, spinner and common dolphins in the eastern tropical Pacific. Estimates for common dolphins are pooled.

Year	Northern spotted	Southern spotted	Eastern spinner	Whitebelly spinner	Common *
1986	4.49	1.90	3.30	1.10	0.76
1987	3.41	0.30	1.77	0.60	0.77
1988	2.38	0.80	3.20	0.40	0.51
1989	3.44	1.50	2.60	0.80	0.45
1990	2.13	0.60	0.90	0.70	0.16
MEAN	3.2	1.2	2.4	0.7	0.5

* Northern, Central, and Southern stocks

reported on trends (5-yr moving mean) between 1975 and 1987. The only significant trends were for the northern stock from 1975 to 1979 (declining) and the southern stock from 1982-1986 (declining). Edwards and Perkins (1991) investigated the likelihood of trends over all of the data published by Anganuzzi and Buckland (1989) using a 10-yr moving mean. Significant declines were found only for the northern offshore stock in years 1975-1984 and 1976-1985. A power analysis with type 1 and type 2 error levels set at 0.1 indicated that significant trends would have had to be on the order of a 5-6% decline per year over the 10-yr period, to be statistically detectable.

A more recent analysis by Anganuzzi et al. (1992b), using smoothed indices of abundance following the methods proposed by Buckland et al. (1992), indicated that the number of animals in the northern stock of the offshore spotted dolphin was more or less stable between 1986 and 1990. A similar pattern was reported for the southern stock, except that the 1990 index of abundance was substantially greater than preceding indices. Anganuzzi et al. (1992b) reasoned that this latter estimate was influenced by large-scale movements of animals from the northern stock.

If there were no incidental mortalities of spotted dolphins in the purse seine fishery, we would expect the northern and southern stocks of this species to recover to prefishery levels at a rate of approximately 2-6% per year (see Reilly and Barlow 1986). The northern stock would take substantially longer to recover because it was presumably exploited to a greater extent than the southern stock. For the northern offshore stock, the current rate of incidental mortality approximates the expected rate of increase. Therefore, it is not surprising that significant trends in abundance have not been detected in recent years. The lower kill rate of the southern stock would still reduce the rate of recovery to a level that would be difficult to detect over a 5-yr period.

SPINNER DOLPHIN

Distribution and stock structure

There are currently four recognized stocks of spinner dolphins in the ETP (northern whitebelly, southern whitebelly, eastern, and Costa Rican) (Anonymous 1987). Due to the high degree of overlap in distribution between spinner dolphin stocks, Perrin et al. (1985) recommended the following changes to the existing stock definitions: (1) south of 16°N, north of 7°N and within 81 km of the coast, schools of spinner dolphins should not be assigned to a stock by position alone, but rather by modal length and relative beak length; and (2) identification of spinner schools as eastern or whitebelly should be based on modal adult color pattern or adult-male dorsal-fin shape or both. Perrin (1990) suggested that the northern and southern whitebelly stocks should be combined into a single management unit. Subsequent references to whitebelly spinner dolphins in this paper will follow this recommendation.

Population estimates

Holt and Powers (1982) estimated abundance levels for eastern spinner dolphins in 1979 (Table 2) as 292 900 (RVD) and 292 700 (RVTVD) with CVs of 22 and 24%, respectively. Based on the first 4-yr of the MOPS surveys (Table 3: 1986-1989) Sexton et al. (1992) and Gerrodette and Wade (1992) estimated abundance of the eastern stock to be between 707 200 and 1 200 100 with an average for the 4-yr of approximately 881 200. CVs were approximately 20% in all years. Wade and Gerrodette (1992) estimated the eastern spinner abundance based on the five MOPS surveys (Table 4: 1986-1990) to be between 391 200 and 754 200 with CVs between 37 and 42%. Wade and Gerrodette's (1992) average estimate for 5-yr of data was 588 500. Tuna vessel observer data (Table 5) yields relative abundance estimates in the range of 376 000 to 717 000 between 1986 and 1990, averaging 490 000 (Anganuzzi and Buckland 1989, Anganuzzi et al. 1992a,b). Because U. S. fishermen are not allowed to set on pure schools of eastern spinner dolphins, and therefore are less likely to chase and identify these schools, it is not surprising that estimates of abundance based on tuna vessel data for this stock are slightly lower than those from research vessels.

Abundance estimates for the whitebelly stock (Tables 2 and 3) varied between 570 200 and 607 000 (RVD and RVTVD, respectively) in 1979 (Holt and Powers 1982: CV=25%) and 657 200 to 1 170 100 between 1986 and 1989 (Sexton et al. 1992, Gerrodette and Wade 1992: CV approximately 20%). Wade and Gerrodette (1992) reported abundance estimates for the whitebelly stock (Table 4) ranging from 363 300 to 1 398 400 with CVs between 38 and 64% and an average estimate for the 5-yr of 993 700. Tuna vessel observer data has provided relative abundance estimates ranging from 451 000 to 705 000, and averaging 610 600 for the years 1986-1990 (Table 5).

Mortality estimates and mortality rates

Incidental mortality estimates for the eastern stock declined between 1986 and 1990 by an average of 2341 animals per year ($P=0.26$; Table 1). Between 1986 and

1990, mortality averaged 13 860 animals per year. The estimated level of mortality, expressed as a percent of population size (based on MOPS data; Wade and Gerrodette 1992), declined from 3.3% in 1986 to 0.9% in 1990 (Table 6). For the whitebelly stock, estimated mortality has been much lower than for the eastern stock both in numbers and as a percent. Between 1986 and 1990, mortality varied between 3500 and 11 000 per year (Table 1). The mortality rate has not exceeded 1.1% in recent years (Table 6).

Assessment and status

Anganuzzi and Buckland (1989) reported a significant increase in abundance between 1982 and 1986 and a significant decrease between 1975 and 1979 for eastern spinner dolphins. Edwards and Perkins (1991) detected no significant trends over four 10-yr periods (1975/1984, 1976/1985, 1977/1986, and 1978/1987). However, consistent with Anganuzzi and Buckland's results, during the first two 10-yr periods, the slope of the regression was negative (i.e., population declining), while during the second two periods the slope was positive (i.e., population increasing). The 1989 smoothed index of abundance of Anganuzzi et al. (1992b) was not significantly different from any of the earlier years. As was the case for the northern spotted dolphins, the current rate of incidental mortality is similar to the expected rate of recovery. Therefore, in view of the variance associated with the indices of abundance, it is not surprising that trends in abundance have not been detected.

Anganuzzi et al. (1992b) reported that the whitebelly stock has shown "little evidence of any recent trend in abundance" since 1983. Between 1976 and 1983, they reported detecting a decline in abundance.

Estimates of historic abundance of eastern spinner dolphins were produced by Wade (1991) based on recent estimates of population size, back-calculation techniques, and input parameters of Smith (1983). This is the only stock whose entire distribution is within the MOPS study area, and, therefore, at least incomplete coverage does not introduce bias into the estimate of abundance. Wade found that over the range of parameter estimates explored, relative population size (defined as the current abundance estimate [N_c] divided by the historical abundance estimate [N_h]) is most sensitive to initial population abundance. Starting the population at 391 200 versus 754 200 (lowest and highest N_c used in simulations), which is equal to the range in population size estimate from Wade and Gerrodette (1992), resulted in a 12-27% increase in relative abundance. Of even more significance was the range over which relative population sizes change. Whereas Smith (1983) estimated relative population size for the eastern spinner dolphin population to be from 0.17 to 0.25, Wade (1991), using an N_c of 391 200, estimated relative population sizes from 0.21 to 0.33, and using an N_c of 754 200, estimated relative populations sizes to be from 0.33 to 0.60.

For ETP dolphins the results of back-calculation models are confounded by lack of information on which to estimate mortality for the period 1959-1972 (see Lo and Smith 1986, Smith and Lo, 1983). Repeating the above calculations using mortality estimates 20% lower and 20% higher resulted in estimated relative population sizes from 0.18 to 0.41 using an N_c of 391 200, and estimated relative population sizes from 0.29 to 0.73 using an N_c of 754 200 (Wade 1991). It is not possible at this time to ascertain whether

the range of mortality estimates used by Wade (1991) includes the actual level of eastern spinner dolphin mortality between 1959 and 1972.

COMMON DOLPHIN

Distribution and stock structure

Presently there are three recognized stocks of common dolphins taken by the U. S. fleet in the ETP (northern tropical, central tropical, and southern tropical) (Anonymous 1987). Perrin et al. (1985) recommended changing the existing definition within 162 km of the coast of Baja California and in the Gulf of California, such that common dolphins should be identified to stock as Baja neritic or northern based on modal length, coloration, and relative beak length. Reilly (1990) recently reported that common dolphins do not seem to have seasonal shifts in distribution centers, as do spotted and spinner dolphins. Rather, common dolphin stocks occupy year-round density centers in areas of upwelling near the Revillagigedos Islands, along the coast of Baja California and Ecuador, and near the Costa Rican Dome. The extent to which this pattern of distribution confounds traditional stock identification methods is currently being examined by NMFS.

Population estimates

Holt and Powers (1982) estimated the total number of common dolphins in the ETP (Table 2) to be approximately 921 000 (RVD) and 1 373 100 (RVTVD). Estimates of abundance from the first 4 yr of MOPS (Table 3) ranged from 163 200 to 836 900 for the northern stock, 619 600 to 3 177 400 for the central stock, and 243 500 to 1 248 700 for the southern stock. Abundance estimates of common dolphin stocks made by Wade and Gerrodette (1992) based on MOPS data from 1986 through 1990 were between 23 500 and 1 272 400 for the northern stock, 261 000 and 1 487 600 for the central stock, and 152 000 and 3 664 000 for the southern stock (CVs between 50 and 77%, Table 4). The average estimate of abundance for common dolphins, pooled over all stocks between 1986 and 1990, was approximately 3 179 000 (Table 4).

Differences between some of the annual estimates for this species from MOPS surveys are probably great (see Table 4). It is possible that the variance has been underestimated, that there was extensive immigration of animals from the south or west into north and central areas, or that bias in the abundance estimate was not constant from year to year (or all of the above).

The estimated average abundance based on tuna vessel data from 1986 through 1990 pooled over all stocks was 575 800 (Table 5). Abundance estimates for the three stocks of common dolphins were for 1990: northern stock 281 000, central stock 87 000, and the southern stock 139 000 (Anganuzzi et al. 1992b). The range of abundance estimates from tuna vessel and research vessel data was 364 000 to 817 00 and 523 000 to 5 656 500, respectively.

Mortality estimates and mortality rates

Mortality estimates for the three stocks are highly variable from year to year, but considerably less in absolute number than for northern offshore spotted dolphins or eastern spinner dolphins. Quotas for U. S. fishermen exist for all three stocks (northern stock 1890, central stock 8112, and southern stock 4045)(Anonymous 1987). In recent years, the central stock has suffered the greatest absolute amount of incidental mortality of the three common stocks.

Assuming the abundance of each stock has remained constant, the average estimate for the years 1986-1990 can be used to determine the annual mortality rate for each stock. Because of uncertainty in estimating the abundance of common dolphin stocks, their abundance estimates have been pooled. The average mortality rate decreased from 0.76% in 1986 to 0.16% in 1990 (Table 6). The average mortality rate is approximately 0.5%, pooled over all 5 yr and all three stocks.

Assessment and status

Anganuzzi and Buckland (1989) reported only one significant decline during a 5-yr period for any of the three stocks of this species: the central stock declined between 1977 and 1981. Edwards and Perkins (1991) reported a significant increase in the northern stock between 1975 and 1984 and significant decreases in the central stock between years 1975 and 1984, 1976 and 1985, and 1978 and 1987.

The most recent analysis of sightings data from observers aboard tuna vessels indicates that all three stocks declined between the late 1970s and 1989 (Anganuzzi et al. 1992b). Since 1985, there has been no indication of significant trends for any of the three stocks. Based on the analysis of Anganuzzi et al. (1992b), the increase in the northern stock between 1975 and 1984 reported by Edwards and Perkins (1991) is likely an artifact of the very low abundance estimate for 1975.

DISCUSSION

Since the early 1970s, over 1.25 million dolphins have been incidentally killed in purse-seine fishing for yellowfin tuna in the ETP. Over half of this take has been composed of northern offshore spotted dolphins; at least 80% of the take is northern offshore spotted dolphins and spinner dolphins. Currently, fishermen take significant numbers of spotted (northern and southern offshore stocks), spinner (eastern and whitebelly stocks) and common dolphins (northern, central, and southern stocks). Over the last 5 yr, the total estimated dolphin mortality has decreased from 133 174 animals in 1986 to 52 531 animals in 1990. Based on annual estimates of stock specific mortality and the average population size of stocks from the recent series of five research vessel surveys over the last 5 yr, the average estimated percent mortality has exceeded 2% of stock for eastern spinner dolphins and northern spotted dolphins and less than 2% per year for all of the other stocks. Because stock-specific rates of incidental mortality have

been declining since 1986, the current levels of take of individual stocks are likely to be sustainable. This interpretation is supported by the available information on trends in abundance.

Based on an analysis of smoothed abundance indices, all of the stocks of ETP dolphins that interact with the tuna fishery have been more or less stable since 1985. The only exception is the southern stock of offshore spotted dolphins which may have increased during this period. However, over the last 15 yr, significant declines in abundance have been reported for stocks of the northern and southern offshore spotted dolphin, the whitebelly stock of spinner dolphins, and the northern, southern, and central stocks of common dolphin. The eastern stock of spinner dolphin has been relatively constant over the last 15 yr. Apparently most of this decline occurred in the years prior to 1985.

Concerning future management practices, the authors note the following: (1) geographically defined management units are not necessarily biologically meaningful, (2) abundance can be estimated for a management unit, but trends in abundance must be determined by pooling stocks that are thought to mix or overlap in distribution, and (3) where quota management is considered appropriate, quotas should be established for each management unit. The management of dolphin stocks in the ETP will likely be most effective if future decisions are based on both the results of trend analysis and estimates of fishery caused mortality expressed as a percentage of population size. The former takes advantage of a long time series of tuna vessel observer data, while the latter can be used to prevent additional declines or to encourage depleted stocks to recover.

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PROS AND CONS OF PINNIPED MANAGEMENT ALONG THE NORTH AMERICAN COAST TO ABET FISH STOCKS

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Abstract. In this paper, we discuss the merit (or lack, thereof) of controlling pinniped populations for the purpose of enhancing fish stocks. Inherent in this approach is the assumption that predation by pinnipeds limits net production of at least some fish populations and, that any net surplus in production, caused by a culling program, can be effectively utilized in commercial harvests. Four generally accepted ecological relationships work against the success of culling pinniped herds to enhance fishery production. First, prey species almost always have more than one predator. Second, pinniped species rarely are dependent on only one species of prey. Third, the recruitment rate of most fish stocks is highly variable, and this is one of the most likely factors determining stock abundance. And fourth, fish, as a predatory group, consume more fish than do other predators (e.g., seabirds, cetaceans, and pinnipeds). Two examples of control programs and their effects on local fisheries are discussed. The following information is necessary to evaluate the biological merits of a pinniped control program (excluding ethical considerations and public sentiment): (1) kind, size, and amount of target species taken by pinniped species (by age, sex, and area), by other predators, by commercial fisheries, and by recreational fisheries and how knowledge of these takes will be effected by the management program; (2) standing stock, trends in stock size, and the relationship between net production and standing stock of the target species; (3) population size, trends in abundance, status, and net production of pinniped species; (4) expected increase in yield (and confidence levels) resulting from cull, and value of this increase in net production to the fishery and the general public; (5) cost of the control program; (6) proposed number (by age and sex classes) of pinnipeds to be culled each year, and the duration of the cull in years; and, (7) long-term effect of the cull on the pinniped population. It is unlikely that information on points (1), (3), and (4) will ever be known with reasonable confidence. Statistically designed removal experiments may be the only method of determining the merit of a control program. Unfortunately, it will be difficult to generalize results from one such experiment to other areas, species, or fisheries.

INTRODUCTION

Multispecies or ecosystem management requires managers to decide: (1) the optimal species composition in a given community and, (2) the degree to which the existing species community can be manipulated (May et al. 1979). Inherent in controlling pinniped populations for the purpose of enhancing fish stocks is the assumption that predation by pinnipeds limits the net production of at least some fish populations, and that any net surplus in production caused by a culling program can be effectively utilized in the commercial harvests. To date, specific cases where this assumption has been met have only been reported for a fresh water system (Power and Gregoire 1978). In this paper we provide an additional case.

In 1981 a workshop was held in La Jolla, California to review the relations between marine mammal populations and their prey, some of which are of commercial and recreational value to fishermen (see Beddington et al. 1985). The workshop participants concluded that there were no unambiguous examples in which marine mammal predation has affected the abundance of a commercial fish stock (Beverton 1985). This conclusion, as applied to west coast and Alaskan pinnipeds, was based on reports by Lowry and Frost (1985), Swartzman and Haar (1985), and DeMaster et al. (1985). It was further reported at this workshop that pinniped-fishery interactions can be significant, and have been well documented. These include cases where pinnipeds damage gear or fish caught in fishing gear, or frighten fish away from traditional fishing grounds (DeMaster et al. 1982, Beach et al. 1982). In 1983, another workshop was held in Anchorage, Alaska to evaluate the interactions between marine mammals and fisheries in the southeastern Bering sea (Melteff and Rosenberg 1984). The participants of this workshop concluded that the available information on the number and diet of marine mammals was insufficient to evaluate the extent to which marine mammal predation on fish may affect a fishery.

In the absence of data needed to make predictions about the effects of seal predation on a fishery, one would hope the scientific literature might provide experimental evidence. However, there are very few publications or references describing seal control programs that were coupled with adequate monitoring programs to determine whether both the pinniped and fish populations responded as predicted. One such example is given by Harwood and Greenwood (1985), where in 1963 a Consultative Committee on Grey Seals and Fisheries recommended that grey seal (*Halichoerus grypus*) populations in the Orkney and Farne Islands be reduced to three-quarters of their current size by killing pups during the breeding season. While several culls did take place, the populations continued to increase. In 1976, a new management scheme was introduced to reduce the grey seal population of the Outer Hebrides and Orkney from 50 000 to 35 000 animals over a five-year period. This second control program involved the taking of cows and pups. However, after one year, the cull was discontinued because of public protest. Fur seal control programs are described also by Shaughnessy (1985) and Swartzman and Haar (1985). Again, the effect of the cull on fish stocks could not be determined in either case. Unfortunately, pinniped control programs are historically associated with periods of extremely variable, usually increasing, fishing effort, which confounds an analysis of the effect of the seal cull on the fish stock.

Therefore, progress in evaluating the efficacy of pinniped control programs to enhance fish stocks has remained elusive over the last ten years. This failure stems in part from a lack of support from the general public for continuing seal control programs long enough (if at all) to adequately test their effects, inadequate control of fishing effort immediately following the initiation of culling, and the inherent variability in fish recruitment. The underlying premise in this paper is that pinniped management programs specifically directed at benefiting a commercial fishery should be considered only if they meet the following criteria: (1) it must be possible to estimate with confidence intervals, how much larger the yield would be from the fishery in question if the pinniped population were reduced by a specified amount, other things being equal, (2) the number of pinnipeds by age and sex class that have to be removed from the population each year to maintain the post-treatment population level must be specified, and (3) the cost of pinniped management must be significantly less than the minimum estimated value of the increase in fishery production.

Throughout this paper we have avoided the issue of whether it is ethical to manipulate marine ecosystems. That is, we have assumed that managers will initiate only seal control programs that meet the above criteria and that final decisions concerning implementation will be "negotiated" among all of the user groups. Proposals to manipulate seal populations where there is no economic gain presumably will be dismissed. Attempts to garner public acceptance of seal control programs should only proceed for those situations where economic gains are expected based on sound scientific analyses. A final decision to proceed should incorporate the expected response of the public, because such programs will likely require a minimum of five years to show any affect on fish abundance or fishery yields.

The remainder of this paper will be directed at a general evaluation of each of these criterion and the application of these criteria to west coast pinniped-fishery interactions.

*Determination of how much larger the yield would be
from the fishery if the pinniped population were reduced*

To date, none of the pinniped control programs have been preceded by what would currently be considered adequate statistical analysis. The intriguing similarities between traditional experimental design, with its assurance of specified confidence intervals, and the recent advances in using credibility intervals (see Press 1989), based on Bayesian theory, indicate that there is more than one approach that can be used to evaluate the merits of a pinniped control program. In any event, information needed to estimate the expected increase in yields and, the posterior distribution of yields must be available. Clearly, there are few marine mammal-fishery interactions presently available where data on the posterior distribution of yields would be informative.

We have identified four generally accepted ecological relationships between predators and prey that confound precise estimation of increases in yield resulting from pinniped control programs. First, prey species almost always have more than one predator. Expected gains in yield by reducing one predator population can be offset by functional or numerical responses (Holling 1970) in other predator populations. Second, predator species rarely are dependent on one species of prey. Therefore, predicting the

predation rate on a particular species will undoubtedly be area and time-specific. Third, the recruitment rate of most fish stocks is highly variable, and it is one of the most likely factors controlling stock abundance. Because stock-recruitment relationships for most commercially valuable fish are obscure (Houde 1989, Sissenwine et al. 1984), it is unlikely that we will be able to predict, with adequate precision, the effect of removing pinnipeds on the recruitment rate. Furthermore, at least some populations of pinniped prey species are greatly affected by storms that disrupt the distribution of forage (Lasker 1975). This interaction is mediated through the larval stage (at least for anchovies, *Engraulis mordax*) and is, therefore, relatively independent of pinniped predation on older age classes. And fourth, fish, as a predatory group, consume more of gross fish production than do other predators (e.g., seabirds, cetaceans, and pinnipeds). For example, Sissenwine et al. (1984) estimated that Georges Bank fish consume over 70% of their own production. Smith (1976) estimated that pinnipeds consumed approximately 15% of anchovy production in the California current (Mammals of the sea 1979: appendix IV). In ecosystems where pinniped predation is only a minor component of total predation, pinniped culls on the order of 25-50% of the estimated equilibrium population (which is the maximum cull that would ever likely be authorized under the existing U.S. Marine Mammal Protection Act) would produce only marginal increases in production. Such marginal increases would be very difficult to detect with statistical confidence.

We believe that adequate information to predict changes in annual yields of fisheries caused by a pinniped management programs will be unobtainable for many pinniped species and, for other pinniped species, control programs will not result in increased yields to fisheries. Nevertheless, there may be specific cases where yield predictions are possible and ecological relationships are such that control programs could conceivably increase fishery yields.

The following information is necessary to predict changes in annual yields: (1) kind, size, and amount of target species taken by the pinniped species (by age, sex and area), by other predators, by commercial fishing, and by recreational fishing, and how variable these predation rates are over time, (2) Standing stock size of target species, trends in stock size, and the relationship between net production and stock size, and (3) Relationship among predation rates on the target species by the pinniped species and other predators, distribution and abundance of target species, distribution and abundance of pinniped species, and distribution and abundance of other predators.

Given the above information, it should be possible to estimate the increase in annual yields over a specified time period that is due to the pinniped control program. It is critical to ascertain item (1) because there are many different types of ecological interactions possible between pinniped and fish species. We have identified six basic types of interactions (Fig. 1), following on work by Beverton (1985). Additional interactions are certainly possible. In three of the six interactions, the net result on the target species of a pinniped control program is equivocal. In two of the six interactions, seal culls are predicted to abet fish stocks, whereas in one interaction, seal culls will actually disadvantage a fish stock. Obviously, it is necessary to understand the primary predator-prey relationships in an ecosystem before it is possible to predict the outcome of reducing the density of one of the predators.

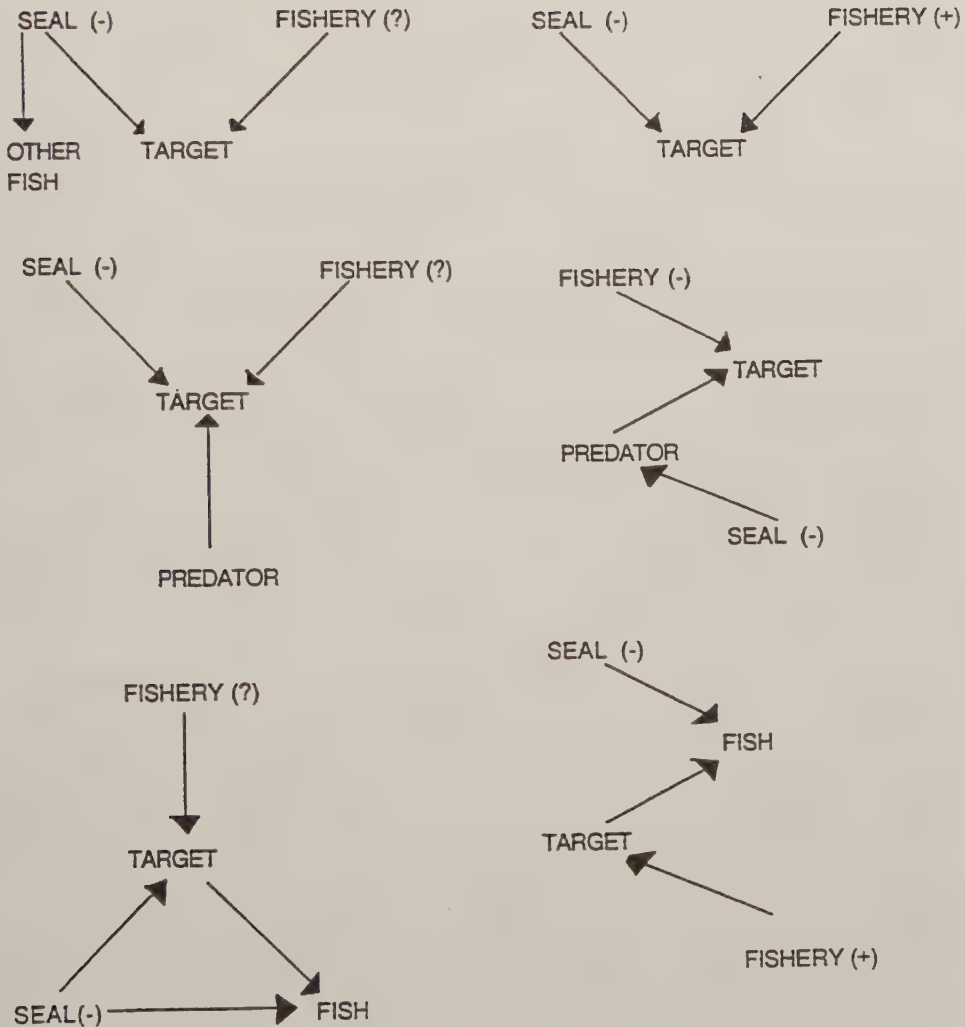


FIG. 1. Six possible ecological interactions among target species, pinniped species, other predator species and fisheries. Minus sign implies reduction in seal populations and fishery yield, plus implies fishery yields will likely increase, and question marks imply fishery yields are equivocal.

Items (2) and (3) will be very difficult obtain in any marine ecosystem. It is relatively straight forward to develop estimates of total consumption by a pinniped species with information on population size, average weight, and an estimate of daily food requirements (Boulva, 1975, Gallivan and Ronald 1979, Geraci 1977, Harwood and Greenwood 1985, Lavigne et al. 1985, and Prime and Harwood 1987), whereas, predicting the amount of individual prey species consumed in a given time period is very difficult. For example, California sea lions (*Zalophus californianus*) are known to feed on a wide variety of prey items (Antonelis and Fiscus 1980, Bailey and Ainley 1981, Antonelis et al. 1983, and Lowry et al. 1991a). However, other than the report by Bailey and Ainley (1981), there is virtually no information relating patterns of prey composition in the diet to relative abundance of prey.

*Specification of the number of pinnipeds to be removed each year
and the duration of the removal program*

The following information is needed to address this criterion: (1) population size of pinniped species, trends in abundance, status, and the relationship between net production and stock size, and (2) proposed post-cull population size of pinniped population.

Given the above information, it should be possible to specify the number (by age and sex classes) of pinnipeds to be culled each year, and the duration of the cull in years to achieve the proposed post-cull population size. It should be recognized that control programs directed at young-of-the-year will necessarily require a longer time to equilibrate than control programs that involve the taking of all age and sex classes. Directing a control program at young-of-the-year will also require removal of significantly more animals than a program directed at mature females. Control programs directed at subadult and adult males will have very little influence on the total population size, but may affect local numbers significantly.

It should also be recognized that control programs directed at reducing pinniped populations, or even maintaining current population levels, will involve large numbers of animals. For example, the California sea lion population in California has been increasing at almost 12% per year between 1983 and 1990, and in 1990 was thought to number in excess of 100 000 animals (M. Lowry, *personal communication*, Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, California). That means the population is growing by over 10 000 animals per year. Using the survivorship schedule from Boveng (1988c), and a current population estimate of 120 000 animals, the mature female segment of this population (i.e., five years or older) includes over 28 000 animals. Control programs directed specifically at mature females would have to take on the order of 2000 animals per year to maintain the population at its current level. The male population that typically migrates north of Point Conception outside the breeding season is similarly estimated to include over 29 000 animals. With the available information, it is not possible to estimate how the distribution of males would change if the male population were reduced in size. It is likely that local changes in abundance could be produced by removal programs, although this effect may be more the result of "harassment from an area" than the absolute number of animals removed from an area.

Populations of northern elephant seals (*Mirounga angustirostris*) and harbor seals (*Phoca vitulina*) along the west coast (i.e., north of U.S.-Mexico border and south of U.S.-Canadian border) are also large (50 000 animals for each species, Boveng 1988a and 1989b). Control programs directed at either of these populations would involve culling of hundreds, if not thousands, of animals per year.

Determination of the net value of the pinniped control program

The following information is needed to address this criterion: (1) expected cost of pinniped control per year over the first five years of the program, and (2) value of minimum expected increase in annual yields of the fishery per year over the first five years of the program.

Given the above information, the "worst case" net economic value of the pinniped program can be estimated. The "worst case" scenario may seem extreme to the fishing industry, but it is consistent with Congressional intent to err on the side of the marine mammal population in the Marine Mammal Protection Act. The need to project costs and economic gains over a five year period (or longer) is necessary for two reasons. First, depending on the age and sex classes of pinnipeds targeted for removal, a lag between initiation of the program and achieving the post-treatment population size should be expected. Second, the annual variability in fishery yields is such that an average over time is needed to characterize the effects of the treatment. As reported by Beverton (1985), "Because the 'improvement' (in fishery yields) is relative rather than absolute does not necessarily diminish its real value, even though its perceived value in terms of stock enhancement may be questioned." That is, the value of the expected increase in annual fishery yield has to be relative to the value of yield in the absence of a predator control program, and not relative to the average or annual yield of a fishery over some fixed period of time.

Case study: California sea lion and fishery interactions along the west coast

As stated earlier in this paper, California sea lions are recovering from over-exploitation in the late 19th and early 20th centuries (Cass 1985, Helling 1984). The number of California sea lions in California at the time the Marine Mammals Protection Act passed was approximately 50 000 animals, based on total pup production and using the same multiplier as Boveng (1988c). The current population size is at least twice that number and is currently increasing. Total consumption of fish by this species at various population levels have been estimated to be 100 000-300 000 tons (DeMaster 1983), 270 000 tons (Smith 1976), and 290 000 tons (Green 1978). Only Green (1978) has attempted to apportion total consumption among the known list of prey species.

California sea lions are unlikely to limit the biomass of any of their prey species. This conclusion is admittedly speculative, but it is based on the following arguments. First, California sea lion prey are generally between 50mm and 250mm in length (Hawes 1983). If the current theories about recruitment of California sea lion prey species are correct, regulation of these species is mitigated through variability in the annual recruitment of larval (and perhaps juvenile) age classes. Therefore, California sea lion predation is affecting age classes that have already made it through the "recruitment

bottleneck." Second, California sea lions are likely constituting a relative small fraction of the total predation on any of their species of prey. Third, fishery landings in California have traditionally exceeded the total estimated consumption by California sea lions. The maximum tonnage per year of landings in California over the last 60 years was over 800 000 tons (O'Bannon 1990), while the maximum consumption by California sea lion in the last 50 years is likely to have been between 100 000 and 300 000 tons. Total landings in California in 1988 and 1989 were 248 000 tons and 209 000 tons, respectively.

California sea lions undoubtedly are causing financial losses to fishermen along the west coast. These losses are caused by California sea lions directly damaging gear and catch, and by their frightening fish away from traditional fishing grounds. However, pinniped control programs targeted at reducing the general population of California sea lions will do little to mitigate these interactions. Only changes in the local abundance of California sea lions or the development of methods to frighten them away from fishing grounds will address this problem.

In general, the only California sea lion control programs that could possibly satisfy the three criteria proposed in this report are those that are directed at local populations. In particular, an evaluation of a control program directed at California sea lion that utilize an endangered run of steelhead (*Oncorhynchus mykiss*) in Puget Sound, Washington seems warranted. A detailed analysis is therefore recommended. Our preliminary analysis suggests that without some type of pinniped control, this population of steelhead will be lost or that recovery will be severely retarded. Because of this, the expected increase of yield following pinniped controls will likely have a low probability of producing negative results. The maximum number of animals to be removed would be on the order of a few hundred individuals (DeLong, *personal communication*, National Marine Mammals Laboratory, Seattle, Washington). The cost of this removal would depend on whether animals were live-captured and translocated or killed. The cost of the former approach likely would be prohibitive. The duration of the control program is difficult to predict at this time but, conceivably, animals would stop utilizing this area as a haul-out and feeding area once culling was initiated. The net value of such a program also is difficult to measure because it involves evaluating the "worth" of recovering an endangered population as well as estimating the value of increasing the yield of this stock from zero to some substantially larger number. Obviously, we are not recommending that such a control program be initiated only that the merits of such a program be evaluated carefully. If the previously mentioned criteria are met, the problems of negotiating this strategy with the general public and surmounting the legal problems, as required under the Marine Mammals Protection Act, will remain significant.

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SPAWNING FREQUENCY AND BATCH FECUNDITY OF CHUB MACKEREL, *SCOMBER JAPONICUS*, DURING 1985

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ABSTRACT

The average female *Scomber japonicus* collected from April through July of 1985 spawned 8.8 times during the 101-day sampling period. The average interval between spawns was 1.3 days in 32 females with more than one spawning stage in their ovary. The average batch fecundity was 68,400 oocytes, or 168 oocytes per gram female wet weight (without ovary).

RESUMEN

Hembras de *Scomber japonicus* colectadas de Abril a Julio de 1985 desovaron en el periodo de muestreo de 101 días un promedio de 8.8 veces. Treinta y dos hembras tuvieron un intervalo promedio entre los desoves de 1.3 días; los ejemplares poseían más de un estadio de desove en sus ovarios. La fecundidad por cada puesta del grupo promedió 68,400 ovocitos, equivalentes a 168 ovocitos por gramo de hembra (peso húmedo; excluyendo el ovario).

INTRODUCTION

Scomber japonicus, chub mackerel, spawn more than once per season (Knaggs and Parrish 1973; Peña et al. 1986; Asano and Tanaka 1989), but the frequency is unknown. The objective of this study was to determine the frequency of spawning and estimate batch fecundity (number of oocytes per spawn) of *S. japonicus*.

MacGregor (1976) believed that the standing stock of yolked oocytes in the ovary of *S. japonicus* before spawning equalled the potential fecundity for the year, a condition called determinate fecundity (Hunter and Macewicz 1985a). But recent studies of other scombroid fishes indicate that fecundity is not fixed at the beginning of year for black skipjack, *Euthynnus lineatus* (Schaefer 1987); skipjack tuna, *Katsuwonus pelamis* (Hunter et al. 1986); or yellowfin tuna, *Thunnus albacares* (Schaefer 1988; McPherson 1991). These fishes spawn many times, yielding annual fecundities far greater than the standing stock of yolked oocytes at the beginning of the spawning season. This latter condition is called indeterminate

annual fecundity (Hunter et al. 1985). It seems certain that the Atlantic mackerel, *Scomber scombrus* L., spawns more than once per season (Bara 1960; Mari-dueña 1984), but debate continues about whether the fecundity of *S. scombrus* is determinate or indeterminate (Macer 1976; Johnson 1977; Alheit et al. 1987; Anon 1987; Greer Walker et al. 1987; Watson et al. 1992; Priede and Watson, in press).

To determine whether fecundity of *S. japonicus* is determinate or indeterminate, we compare the production of spawn over our survey period (batch fecundity $\times$ daily spawning frequency $\times$ survey duration in days) to MacGregor's (1976) estimates of annual fecundity. If *S. japonicus* is determinate, the production of spawn should be lower for our survey period, since we sampled only the peak months of spawning and not the whole season (March to October; Schaefer 1980).

In addition to clarifying the issue of fixed annual fecundity, our estimates of spawning and fecundity rates for *S. japonicus* are of general interest. As a preliminary measure of reproductive effort of the species, they are the baseline data essential for estimating *S. japonicus* biomass from the abundance of eggs or larvae.

METHODS

From April 2 to July 11, 1985, we collected 329 female *S. japonicus* in a series of 30 opportunistic collections taken in the Southern California Bight with hook-and-line or purse seine gear (table 1). All but two of the collections were made during the day, between 0700 and 1510; the two night collections were made between 1955 and 2045 (collection 29) and between 2330 and 0015 (collection 6).

The fish were sexed and measured (fork length), and the females were assigned a maturity stage from the California Department of Fish and Game's (CDFG) standard maturity guide for wetfish (table 2). The guide, based on gross anatomical criteria, is a modified version of the Hjort index (Hjort 1910). Ovaries were removed and preserved in 10% neutral buffered Formalin. The otoliths were removed, and annual growth rings were counted to determine age (year class). Sampling was continued until 20 ran-

TABLE 1
 Number of Female *S. japonicus* per Collection, with
 Histological Identification

Coll. number	Date		Location		Number of females ¹			
	Mo.	Day	°N	°W	Immature	Mature		Total
						A ²	P ³	
1	4	02	33.25	117.38	1	0	0	1
2	4	04	33.43	118.16	2	0	1	3
3	4	05	33.48	118.25	8	3	9	20
4	4	11	33.45	118.09	3	1	11	20
5	4	19	33.44	118.06	3	0	0	3
6	4	21	34.24	119.45	4	0	16	20
7	4	26	33.22	117.36	3	4	3	10
8	5	01	33.45	118.09	3	3	13	19
9	5	05	33.36	117.58	0	5	3	8
10	5	07	33.45	118.09	1	1	3	5
11	5	08	33.24	117.37	0	6	5	11
12	5	09	33.45	118.09	4	0	1	5
13	5	15	33.43	118.16	0	3	17	20
14	5	16	34.27	120.32	0	1	0	1
15	5	17	33.43	118.16	1	5	14	20
16	5	21	33.45	118.09	5	2	7	14
17	5	23	33.43	118.16	0	2	8	10
18	5	30	33.43	118.16	0	0	5	5
19	5	31	33.45	118.09	1	0	7	8
20	6	04	33.45	118.09	1	3	7	11
21	6	05	33.27	117.43	0	7	0	7
22	6	07	33.45	118.09	4	6	10	20
23	6	12	33.27	117.40	0	19	1	20
24	6	21	33.45	118.09	2	3	11	16
25	6	21	33.43	118.14	0	9	1	10
26	6	26	33.27	117.43	5	5	0	10
27	6	30	33.33	117.49	0	8	0	8
28	7	02	33.45	118.09	2	7	11	20
29	7	04	32.47	117.17	0	1	2	3
30	7	11	33.43	118.16	0	1	0	1
All					58	105	166	329

¹All females were collected off southern California in 1985. Collection 6 was taken by purse seine, the rest by hook and line.

²Active: ovaries contain yolked oocytes; if α atresia of yolked oocytes was present, less than 50% of the oocytes were affected.

³Postspawning: ovaries with 50% or more of the yolked oocytes in α -stage atresia, or ovaries without yolked oocytes in which β -stage atresia was present.

dom females had been obtained or until no more fish were available in a particular catch.

Ovaries were prepared according to histological techniques described by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a), and the resulting histological slides were analyzed and classified. Rates of absorption of postovulatory follicles were verified from ovaries of 73 females spawned in the laboratory using procedures of Leong (1971). We also used the histological classifications to evaluate the gross anatomical grading scale routinely used by CDFG to assess the reproductive state of *S. japonicus*. Finally, we estimated batch fecundity, using the hydrated oocyte method of Hunter et al. (1985).

TABLE 2
 Anatomical Classification Used by California
 Department of Fish and Game to Identify Mature
S. japonicus

Stage	Description
[Immature]* 1	Virgin individuals. Very small sexual organs close under vertebral column. Females: often wine-colored, with torpedo-shaped ovaries. Eggs invisible to naked eye. Males: testes very small, knife-shaped, and quite thin. In chub mackerel, testes can be longer than half the ventral cavity.
[Mature]* 2	Maturing virgins or recovering spents. Females: ovaries longer than half the ventral cavity. Eggs may or may not be visible to naked eye. Males: testes easily identifiable, but still thin and knife-shaped.
3	Sexual organs swelling. Eggs definitely visible to naked eye. Ovaries and testes occupying about half the ventral cavity.
4	Ovaries and testes filling nearly 3/4 of ventral cavity. Eggs still opaque. Testes swollen, milt whitish.
5	Ovaries and testes filling ventral cavity. Ovaries often with some large transparent eggs.
6	Roe and milt running. Slight pressure on belly of fish exudes roe or milt.

*Heading not a part of CDFG classification system.

Histological Classification

The oocytes of *S. japonicus* ovaries develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). We used the simplified classification system described by Hunter and Macewicz (1985a,b) to describe the ovaries of *S. japonicus*, instead of the more detailed systems common in teleost literature (see, for example, Andrews¹ or Bara 1960). We categorized the most developed mode of oocytes for each ovary as either unyielded, partially yielded, yielded, or hydrated. We examined the nucleus of the yielded oocytes to see if it had begun to migrate to the animal pole; migration of the nucleus is the precursor to hydration and begins about 24 hours before spawning (Hunter and Macewicz 1985a). After ovulation, the follicles surrounding the hydrated oocytes remain in the ovarian tissue, where they degenerate and are resorbed. All postovulatory follicles were identified and subsequently aged.

The ovarian sections were graded for the presence of alpha (α) atresia of yielded oocytes and grouped into $\alpha < 50\%$ (0 to 49% of the yielded oocytes are in α -stage atresia) or $\alpha \geq 50\%$ (50% or more of the yielded oocytes are in α -stage atresia). Any presence

¹C. B. Andrews. 1931. Unpublished manuscript: The development of the ova of the California sardine (*Sardinia caerulea*). Stanford University, Stanford, Calif. 88 pp.

of beta (β) atresia was also noted. In northern anchovy β atresia follows α -stage atresia of yolked oocytes (Hunter and Macewicz 1985b); we assumed the atretic process was the same in *S. japonicus*. We analysed ovarian atresia (resorption of oocytes) to determine if a female had finished spawning for the season (Hunter and Macewicz 1980, 1985b).

In order to evaluate our histological analyses, it is necessary to define terms for the reproductive status of female *S. japonicus*:

Immature: Females that have never spawned and cannot be expected to do so in the current reproductive season.

Mature: Females that have spawned in the current reproductive season or can be expected to do so.

Active: Mature females capable of spawning at the time of capture or by the end of our sampling period. The ovaries of these females contain yolked oocytes; if α atresia of yolked oocytes is present, less than 50% of the oocytes are affected. Postovulatory follicles may be present.

Postspawning: Mature females incapable of spawning at the time of capture or in the near future but that have spawned previously. Females are considered to be recent postspawning when in their ovaries 50% or more of the yolked oocytes are in the α stage of atresia, and to be late postspawning when there are no yolked oocytes, but β -stage atresia is present in the ovary.

Spawning Frequency

Laboratory calibration. To measure the rate of spawning using postovulatory follicles one must be able to stage the postovulatory follicles according to their age and know how long such stages last. Ovaries from *S. japonicus* induced to spawn in the laboratory were preserved at 0, 6, 12, 18, 24, 48, and 72 hours after spawning, and analyzed. The histological characteristics of *S. japonicus* ovaries are similar to those described for *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980, 1985a,b) and *K. pelamis* (Hunter et al. 1986), except that red blood cells are occasionally observed in the lumen of postovulatory follicles. The degeneration and resorption of *S. japonicus* postovulatory follicles are described below as a function of elapsed time after spawning, when fish are held at 20°C.

0–3 hours: Within a few hours after spawning, no degeneration of the follicle is evident. Other characteristics at this time include a convoluted shape with many folds or loops; a lumen containing little granular or particulate material; a definite

granulosa cell layer lining the lumen; linearly arranged, cuboidal granulosa cells with prominent healthy nuclei; and a clearly defined thecal connective tissue layer with blood capillaries (figure 1).

6 hours: Similar to a 0–3-hour-old postovulatory follicle, except that degeneration of the postovulatory follicle is evident because a few of the nuclei of the granulosa cells are dense or pycnotic.

12–18 hours: Additional signs of degeneration of the postovulatory follicle are evident. The postovulatory follicle is smaller than it was at 6 hours, and it has fewer convolutions. The granulosa layer still comprises numerous cells, although some cytoplasmic vacuoles or granules are present, and cell membranes are less distinct. More of the granulosa nuclei are pycnotic, and the nuclei are not always linearly arranged. The thecal layer appears slightly thicker than at 6 hours because the follicle has compacted.

24 hours: The postovulatory follicle is about half the size of one at 0–3 hours, and the shape is more angular, with fewer folds. The lumen is smaller and may contain red blood cells. The granulosa layer has degenerated further than at 18 hours; there are fewer cells, some pycnotic nuclei, few intact cell membranes, numerous vacuoles, and no alignment of nuclei. The thecal layer remains a distinct, thick band of cells (figure 1).

48 hours: Very few granulosa nuclei remain in the postovulatory follicle. Although the thecal layer appears thick, the follicle is small, about $\frac{1}{3}$ the size at 24 hours, and can be confused with late-stage β atresia (Hunter and Goldberg 1980; Hunter and Macewicz 1985a).

72 hours: The postovulatory follicles are completely resorbed or are indistinguishable from late β atresia.

Analysis of field data. Postovulatory follicles in ovaries of field-caught *S. japonicus* were assigned an age (time after spawning) using the characteristics described above, the time of collection, and the estimated time of peak spawning (about 2200; Schaefer 1980). Twenty-eight collections were taken during the day, when females have oocytes with migratory nuclei, but no oocytes that are fully hydrated. We considered these fish to be capable of spawning on the evening following their capture because we believe that the migratory-nucleus stage persists in the ovary for less than 24 hours, as in Pacific sardine and northern anchovy. We are not able to verify this point because our field samples were taken during the day. But the absence of any fully hydrated oocytes during the day clearly indicates that hydration lasts less than 24 hours.

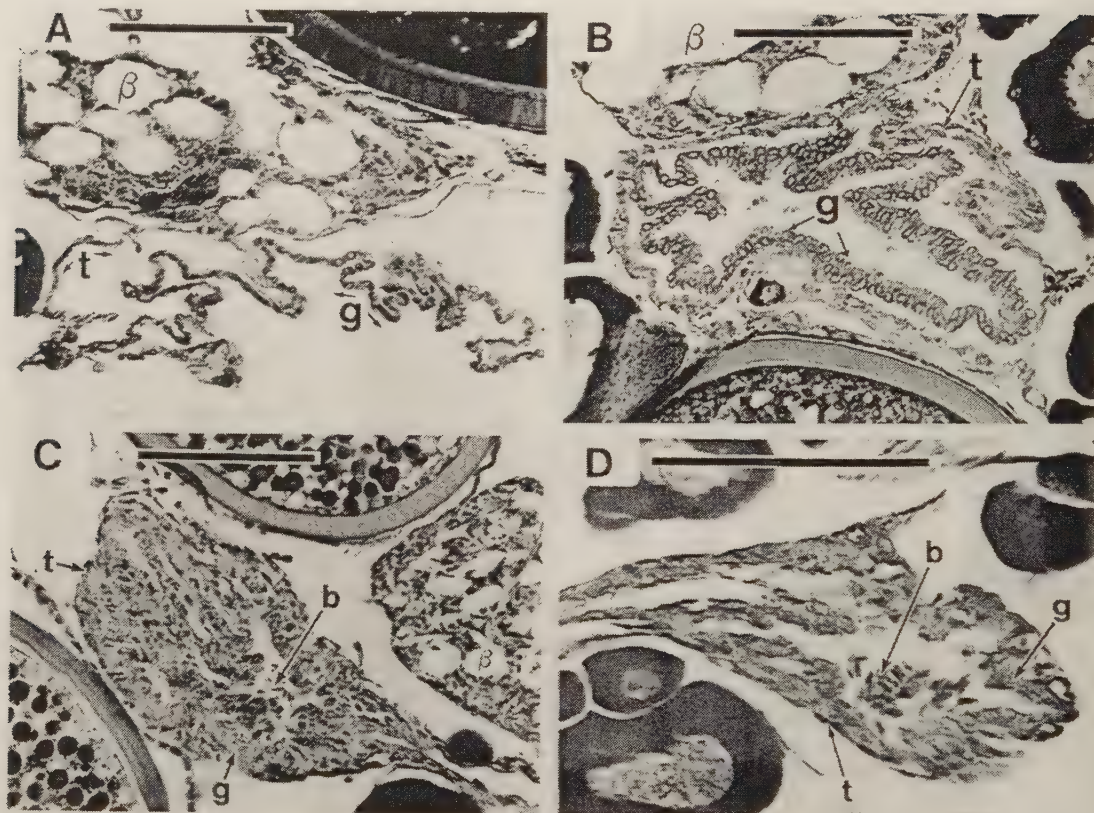


Figure 1. Postovulatory follicles from *S. japonicus* spawned in the laboratory (induced by hormones). No degeneration is evident in A (at ovulation) or in B (1 hour after spawning). By 24 hours after spawning (C and D), degeneration is considerable. Bars = 0.1 mm; b = red blood cells; g = granulosa cell layer; t = thecal connective cell layer; β = beta atresia.

To estimate spawning frequency, we identified in each spawning female the presence or absence of the following:

- oocytes with migratory nuclei
- hydrated oocytes within the follicles
- new postovulatory follicles (0–9 hours) and hydrated oocytes
- postovulatory follicles 10–33 hours old
- postovulatory follicles 34 or more hours old

Some of the ovaries contained more than one age of postovulatory follicles (figure 2); others contained oocytes with migratory nuclei as well as postovulatory follicles. All spawning stages were identified, and any combination of these five stages was recorded for each fish.

Batch Fecundity

We estimated the batch fecundity of 13 females. Batch fecundity for each female was the mean of three estimates. Each estimate was calculated by $(N/T_w)O_w$, where N is the number of oocytes in the late migratory-nucleus stage in a weighed tissue sample of the ovary (T_w), and O_w is the ovary weight (Hunter et al. 1985). Tissue could be taken from any location in the ovary, since Peña et al. (1986) showed that with the hydrated oocyte method, location does not affect the estimate of batch fecundity. The migratory-nucleus stage immediately precedes hydration (Hunter and Macewicz 1985a). Oocytes with migratory nuclei can be seen in Formalin-preserved ovaries because they are larger and less opaque than the other yolked but nonhydrated oocytes, and they

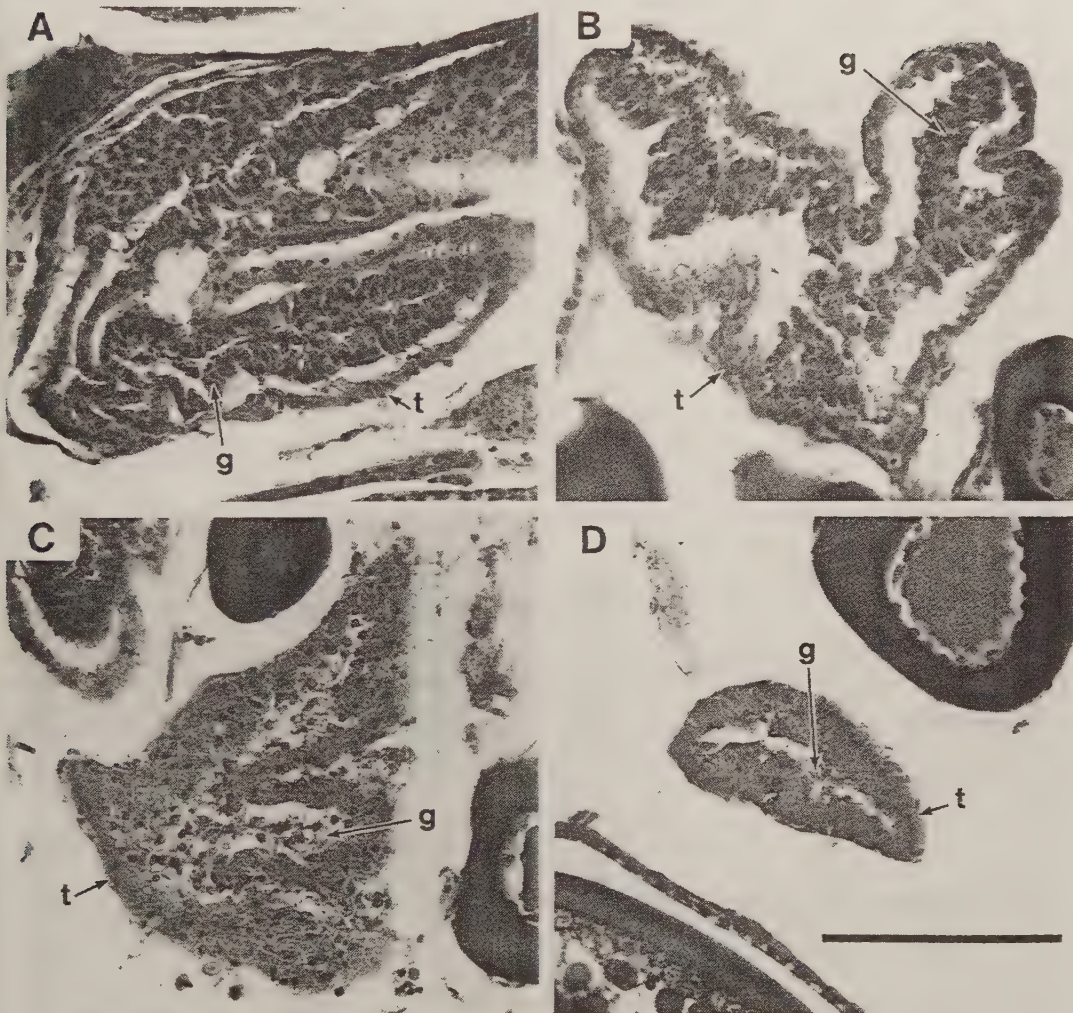


Figure 2. Multiple stages of postovulatory follicles from two *S. japonicus* females collected in the field. Female 9-03 contained postovulatory follicles aged 0–3 hours (A) and about 24 hours old (C) in her ovary. Female 26-06 contained postovulatory follicles about 12 hours old (B) and more than 33 hours old (D). Same magnification for A to D; bar = 0.1 mm; g = granulosa cell layer; t = thecal connective cell layer.

have a clear band on the periphery resulting from the initial fusing of the yolk globules. The more advanced oocytes have a single oil droplet.

RESULTS AND DISCUSSION

Spawning Frequency

Of the 329 female *S. japonicus* analyzed, 271 were mature. Of the mature females, 58 had spawned or would imminently spawn because their ovaries contained postovulatory follicles or oocytes with migratory nuclei (table 3).

The best measures of the percentage of females that spawned per day were the percentage of the mature females having oocytes with migratory nuclei (8.1%), and the percentage of the mature females with postovulatory follicles 10–33 hours old (9.2%). Females with postovulatory follicles older than 34 hours were not used because we were uncertain about their age. Since the oocytes with migratory nuclei and the postovulatory follicles 10–33 hours old indicate different spawning events (figure 3), they can be used as two independent estimates of spawning frequency. The mean of the two estimates

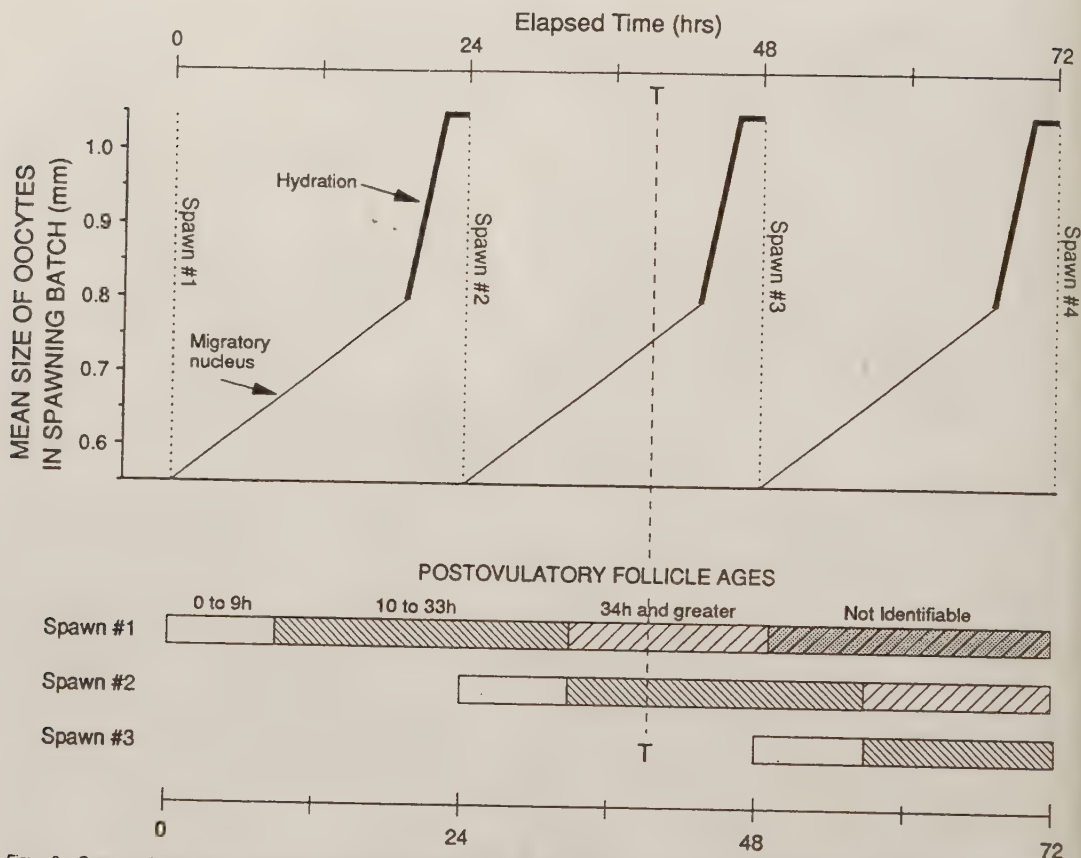


Figure 3. Conceptual diagram showing when various histological stages could be identified in an ovary of an *S. japonicus* female that spawned every day. Stages include migratory nucleus and hydration (0–24 hours before spawning), and postovulatory follicles 0–9 hours old, 10–33 hours old, and 34 hours and older. If a female is collected at time T in the cycle, three spawnings can be identified in the ovary: oocytes with migratory nuclei for spawn #3; 14-hour-old postovulatory follicles from spawn #2; and postovulatory follicles 38 hours old from spawn #1. Stippled area indicates period when postovulatory follicles may be confused with late β atresia.

was 8.7%, indicating that 8.7% of the females spawned per day, or that the average female *S. japonicus* spawned every 12 days. Because the sampling period was 101 days long, this estimate also indicates that the average female spawned 8.8 times during these 101 days.

Most (81%) of the spawning females (those with oocytes with migratory nuclei, or with postovulatory follicles) were collected in June, the month of peak spawning for *S. japonicus* according to the abundance of larvae in CalCOFI plankton collections (Kramer 1960). In June, 20.6% of the females spawned per day, indicating that the average mature female spawned about every five days in June, whereas 2.7% of the mature females spawned per day in May, and 6.8% in July (table 4).

The ovaries of 32 females contained multiple spawning stages. That is, a single ovary contained postovulatory follicles of two different ages, or postovulatory follicles and oocytes with migratory nuclei, or some other combination (table 3). Because we know the approximate age for each of these spawning stages, it is possible to calculate the interval between them. Thus we calculated that the average interval between spawnings for these 32 females was 1.3 days (table 5).

The frequency of spawning tended to increase with female age (table 6). Knaggs and Parrish (1973) concluded that older *S. japonicus* spawn for longer periods than younger ones. In our study none of the mature one-year-old fish were spawning, and only 3.9% of the mature two-year-olds were spawning,

TABLE 3
 Spawning Female *S. japonicus* Taken in the Study ($N = 58$) with Ovaries Indicating Past Spawning
 (Postovulatory Follicles Present) or Imminent Spawning (Oocytes with Migratory Nuclei)

Coll. number	Fish number	Time PST	Year class	CDFG stage	Migratory nucleus	Postovulatory follicles	
						10–33 hours	33 < age < 72 hrs
7	05	0815	1981	5	+	–	–
9	03 ²	1420	1980	6	+	+	+
13	18	1100	1980	3	+	–	–
13	19	1105	1983	2	+	–	–
15	02	1005	1980	4	+	–	+
15	06	1040	1982	3	–	–	+
15	12	1110	1981	4	–	–	+
16	03	0955	1981	3	+	–	–
21	01	1242	1981	3	–	+	–
21	02	1245	1981	3	+	+	+
21	03	1250	1981	3	+	+	+
21	04	1253	1981	3	+	–	+
21	05	1440	1981	2	–	+	+
21	06	1445	1981	3	–	+	+
21	07	1450	1980	4	+	–	+
22	07	0730	1981	2	+	–	–
23	01	1220	1981	3	–	–	+
23	02	1225	1982	2	–	+	+
23	03	1230	1981	3	–	+	+
23	04	1240	1981	4	+	–	+
23	05	1250	1981	3	–	+	+
23	06	1250	1981	3	–	–	+
23	07	1300	1981	3	+	+	+
23	08	1310	1980	4	–	–	+
23	09	1315	1981	4	–	+	–
23	10	1320	1981	3	–	+	+
23	11	1325	1981	3	–	+	+
23	12	1325	1982	3	–	+	+
23	13	1325	1981	4	+	–	+
23	14	1330	1981	3	+	–	+
23	15	1330	1981	3	–	–	+
23	16	1330	1982	3	–	+	–
23	17	1330	1981	3	+	+	+
23	18	1340	1980	4	+	–	+
23	19	1340	1981	3	+	–	+
23	20	1345	1980	2	–	+	–
24	02	0710	1981	3	–	–	+
25	03	0940	1981	3	–	–	+
25	04	1000	1981	3	–	–	+
25	06	1100	1981	4	–	–	+
25	07	1115	1981	3	–	–	+
25	09	1220	1980	4	–	–	+
26	05	1133	1981	3	–	–	+
26	06	1137	1981	4	–	+	+
26	07	1141	1982	3	+	–	+
26	08	1149	1981	4	+	+	+
26	10	1200	1981	4	–	–	+
27	01	1425	1982	2	–	+	+
27	02	1440	1982	3	–	–	+
27	03	1442	1981	3	–	+	+
27	04	1450	1981	3	–	+	+
27	05	1454	1983	3	–	–	+
27	06	1456	1981	2	–	+	+
27	07	1458	1981	2	–	+	+
27	08	1502	1983	2	–	–	+
28	03	0740	1981	3	+	–	+
28	18	1105	1982	3	+	–	+
29	02	2025	1981	4	–	+	+

¹ + indicates that the state was present.

² Ovary had a few hydrated oocytes in the lumen, and new postovulatory follicles, indicating that the female had spawned within the last 0–3 hours, an unusual time of day for *S. japonicus*.

TABLE 4
Percentage of Mature Female *S. japonicus* Classified as Active or Postspawning, and Percentage Spawning per Day

Month	Active ¹ %	Postspawning		Number mature females	Spawning per day		
		Recent ² %	Late ³ %		MN ⁴ %	PO ⁵ %	Mean %
April	17	12	71	48	2	0	1.0
May	25	33	41	111	4	1	2.7
June	67	14	19	90	16	26	20.6
July	41	45	14	22	9	4	6.8
All	39	24	37	271	8.1	9.2	8.7

¹Indicated histologically by presence of yolked oocytes, α atresia <50% of yolked oocytes, and, possibly, postovulatory follicles.

² α atresia is present in 50% or more of the yolked oocytes.

³There are no yolked oocytes in the ovary, but β atresia is present.

⁴Oocytes with migratory nuclei are present in the ovary; spawning is imminent.

⁵Postovulatory follicles are 10–33 hours old; female spawned the previous night.

TABLE 5
Computation of Mean Interval between Spawning for *S. japonicus* Females with Combinations of the Following States in the Ovary: Oocytes with Migratory Nuclei (MN); 10–33-Hour-Old Postovulatory Follicles (PO₁); and >33-Hour-Old Postovulatory Follicles (PO₂)

Spawning states present in ovary	Minimal interval between spawnings ¹ (i in days)	Number females N	Potential days i × N
MN + PO ₁	2	11	22
PO ₁ + PO ₂	1	15	15
MN + PO ₁ + PO ₂	1	6	6
Total		32	43

Average interval between spawnings²: 43/32 = 1.34

¹The interval between spawnings for females with only a single spawning state in the ovary is ≥ 3 days, since 72 hours is the maximum period during which postovulatory follicles can be detected.

²25 females had a single spawning state. If these females were included, the average interval would be 118/57, or 2.07 days.

TABLE 6
Frequency of Spawning of Mature *S. japonicus* Females by Age and Year Class

Age (years)	Year class	Immature N	Mature N	Spawning per day mean percentage ¹
1	1984	11	3	0
2	1983	2	13	3.9
3	1982	10	44	6.8
4	1981	29	166	9.9
5	1980	5	43	8.1
6+	1978 & 1979	1	2	0

¹Calculated from the number of mature females having oocytes with migratory nuclei in their ovaries, and from the number of mature females with postovulatory follicles 10–33 hours old in their ovaries; original data in table 3.

compared to 8.7% for the mature females as a whole. These data support the conclusion of Knaggs and Parrish, but more histological data, sampled over the whole spawning season, are needed to determine spawning by age.

The foregoing analysis indicated that the average female *S. japonicus* may spawn 8.8 times in 101 days, but it is clear that individual females do not spawn at regular intervals over this period. Rather, many of the spawnings must occur in rapid succession at daily or every-other-day intervals. It is interesting to speculate on the possible length of the spawning period for an individual female. If a female spawned 8.8 times at an interval of 1.3 days, the period would be 11.4 days long. If the average interval were 2 days, the period would be 18 days long. The latter period fits the data better because the percentage of spawning females with only one spawning stage (44%) would be too high if the spawning cycle were only 11 days long.

Fecundity

The average batch fecundity for the 13 females having oocytes with migratory nuclei was 68,400 oocytes, or 168 oocytes per gram of female wet weight, without ovary (table 7). By multiplying the mean batch fecundity by the number of spawnings (8.8) we find that a female averaging 444 g would spawn about 602,000 oocytes during the 101-day survey period. This estimate is nearly five times higher than MacGregor's estimate of 126,000 oocytes for the annual fecundity of a 444-g female. Clearly, the standing stock of advanced oocytes does not indicate potential annual fecundity; consequently, we consider the annual fecundity of *S. japonicus* to be indeterminate.

The average Peruvian *S. japonicus* (281 g, without ovary) was estimated to have a mean relative batch fecundity of 278 oocytes per gram (Peña et al. 1986). This is somewhat higher than our estimate of 168 oocytes per gram for a 444-g female. Owing to high variability and few observations, it is uncertain if these differences reflect actual differences between stocks.

TABLE 7
 Batch Fecundity (Number of Oocytes to Be Spawned in the Batch) of Thirteen *S. japonicus* Females
 with Oocytes in the Late Migratory-Nucleus Stage

Coll. & fish number	Time of day collected	Fork length (mm)	Body weight without ovary (g)	Ovary weight (g)	Batch fecundity	
					Per female	Per g body wt
7-05	0815	324	416.79	34.77	85,566	205.3
15-02	1005	319	382.64	46.56	120,537	315.0
26-08	1149	326	424.29	36.44	92,405	217.8
23-04	1240	310	355.32	35.59	69,930	196.8
21-03	1250	340	496.01	32.54	74,723	150.6
21-04	1253	315	380.92	30.95	57,247	150.3
23-07	1300	320	407.68	25.93	47,801	117.3
23-13	1325	301	320.83	34.22	72,338	225.5
23-14	1330	320	409.68	23.32	36,510	89.1
23-17	1330	300	328.45	22.76	35,807	109.0
23-18	1340	340	494.53	34.01	80,807	205.3
23-19	1340	326	438.70	22.03	23,280	53.1
21-07	1450	340	481.64	46.90	91,680	190.4
Mean					68,356	168.0

Our batch fecundity of *S. japonicus* (168 oocytes per gram body weight, without ovary) is about three times that estimated for *S. scombrus*, which ranges from 28 to 55 oocytes/g body weight (Alheit et al. 1987; Watson et al. 1992). This difference between species may be partly due to differences in egg size. The *S. japonicus* egg is about 1.0 mm in diameter (Kramer 1960; Fritzsche 1978); the *S. scombrus* egg is about 1.2 mm (Russel 1976; Fritzsche 1978). The ratio of the diameter cubed for the two species is 1:1.7, indicating that the egg mass of *S. scombrus* may be nearly twice that of *S. japonicus*. Thus the differences in batch fecundity may be explainable in part by differences in egg size, assuming that the energy investment per batch was about the same in the two species. Although this is a plausible explanation, it is certainly speculative, because we have no true mean egg size for either population at present. Egg size of both species varies considerably between localities and seasons, making accurate comparisons difficult.

Atresia

Alpha atresia of the advanced yolked oocytes was common throughout the spawning season. Even early in the season (April) 12% of the females were classed as recent postspawning because of the high levels of α -stage atresia (table 4). Anchovy usually do not spawn when their ovaries are in this advanced state of atresia (Hunter and Macewicz 1985b), and we presume this is also the case for *S. japonicus*. In addition, the atretic condition that follows this state, late postspawning (table 4), was common in *S. japonicus* throughout the spawning season.

Hunter and Macewicz (1985b) believe that highly atretic ovaries are a normal occurrence in the annual reproductive cycle in fishes with indeterminate fecundity. They conclude that highly atretic ovaries indicate fish that have ended their reproductive season, and should be considered as synonymous with "spent," or postspawning, ovary classes. High levels of atresia might be induced by abnormal events such as an epidemic or environmental stress rather than by the normal cessation of spawning, but we believe that the normal cessation of spawning is much more likely. It is also possible that during a single spawning season *S. japonicus* may pass through more than one cycle of oocyte maturation, spawning, and atresia.

The most striking feature of our data on atresia was that females with highly atretic ovaries were common early in the spawning season. In anchovy, this condition is prevalent only near the end of the season, when spawning is declining for the stock as a whole. The prevalence of atresia indicates that the spawning cycles of *S. japonicus*, unlike those of the anchovy, are not synchronized for the stock as a whole but rather seem to vary from sample to sample. Spawning may be synchronized at some lower level of organization than the stock, such as the school or school group (Smith 1975). Alternatively, schools may segregate according to behavioral traits, with spawning schools occupying different areas from postspawning schools.

Regardless of the mechanisms involved, the patchiness of spawning individuals indicates that obtaining representative samples of an *S. japonicus* stock may be very difficult. Considering the patch-

iness of spawning and postspawning females and the fact that our sampling was opportunistic, our samples may not accurately represent spawning rate of the stock over the 101 days. Since many females spawned at intervals of every 1.3 days, and in June the average female spawned every 5 days, we believe that our estimate of 8.8 spawns per year for the average female may be low.

Evaluation of Anatomical Classification of Ovaries

To determine the value of classifying ovaries by means of gross anatomical criteria, we used the Hjort maturity index modified by CDFG (table 2) as well as histological criteria to classify the *S. japonicus* ovaries (table 8). CDFG considered only stage 1, in table 2, as immature, and stages 2–6 as mature. Histological analysis indicated that the mature females occurred in all stages (table 8). On the basis of the histological evidence, the misclassified immature females in stage 1 were considered to be in postspawning condition, because they were resorbing their ovaries. Surprisingly, the percentage of all females classed as mature was similar regardless of the method used to classify them. When anatomical criteria were used, 90% of all females were estimated to be mature; when histological criteria were used, 82% were mature. The failure to detect postspawning females using anatomical criteria was counterbalanced by histological identification of immature females in CDFG stages 2 and 3.

Spawning females occurred in every anatomical stage except stage 1 (tables 3 and 8). But according to CDFG criteria, spawning females occur only in stages 5 and 6 (table 2). Clearly, the CDFG anatomical criteria do not identify all the spawning females.

Although anatomical staging is useful when studying a population (e.g., the duration of spawning seasons), it is inaccurate when considering indi-

vidual fish. Our findings agree with those of Asano and Tanaka (1989), who studied reproduction of the Japanese stock of *S. japonicus*. They concluded that females with active ovaries, those actively spawning, and those in postspawning condition cannot be accurately separated if only anatomical criteria are used. Similarly, West (1990) states in his review that macroscopic staging may result in unacceptably high errors when used to examine the ovarian development of an individual fish.

Histological methods obviously provide more detailed and accurate assessments of fish maturity and reproduction. There will always be a need for gross anatomical methods because of the speed and ease that they offer. We believe that the six-stage anatomical grading system of CDFG needs revision. With the unaided eye, only three characteristics actually can be detected: (1) yolked oocytes not present, (2) yolked oocytes visible, and (3) hydrated oocytes visible. The rest of the characteristics used are unreliable or imply knowledge of maturity and spawning that the observer does not have; thus, we recommend a three-stage system.

CONCLUSIONS

Our estimate of spawning rate for the population of *S. japonicus* is lower than one would expect from information available about other scombroid fishes. We estimated that 8.7% of *S. japonicus* females spawned per day, whereas estimates for most other scombroid fishes indicate that they spawn at much higher rates. For example, 85% of female skipjack tuna spawn per day (Hunter et al. 1986); 18%–47% of black skipjack spawn per day (Schaefer 1987); 80% of yellowfin tuna spawn per day (Schaefer 1988); and 18%–62% of *S. scombrus* spawn per day (Priede and Watson, in press). We suspect that the actual rate of spawning of *S. japonicus* females may

TABLE 8
 Comparison of California Department of Fish and Game Anatomical Maturity Classification and Histological Classification of the Ovaries of *S. japonicus* Collected in 1985

Number of females	Anatomical classification ¹		Histological classification			
	Stage number	Fish maturity	Immature %	Mature		
				Postspawn %	Nonspawn %	Spawn %
34	1	Immature	44	56	0	0
174	2	Mature	23	68	3	5
91	3	Mature	3	29	32	36
26	4	Mature		4	42	54
2	5	Mature		0	50	50
1	6	Mature		0	0	100
Fraction mature:		294/328 = .90		270/328 = .82		

¹See table 2 for description of stages.

have been much higher for four reasons: (1) our opportunistic sampling may have biased our estimate; (2) females with multiple stages in the ovary spawned every 1.3 days; (3) our studies of atresia indicated that the distributions of postspawning and spawning females may have been highly contagious; and (4) our samples did not adequately cover the entire spawning season.

We believe that our estimates of a spawning rate of 8.7% of the female population per day and 8.8 spawnings per year for the average female are low. We hope this paper will encourage others to carry out a thorough study with a formal sampling design that takes into account age and size patterns in spawning rate, batch fecundity, and duration of the spawning season.

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Rethinking the Stock Concept: A Phylogeographic Approach

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Abstract: The "stock" is the fundamental population unit of legally mandated conservation efforts, yet its formal definition in the scientific literature and in two U.S. conservation acts is varied and so general that attempts to apply it in practice are arbitrary. Because choice of stocks deserving management protection is sometimes politically contentious, improvement of the working definition is important.

A key element should be the degree to which a population can be considered an evolutionary significant unit. We propose that a hierarchical classification scheme be applied to stock designations. Category I populations, having the highest probability of being evolutionarily significant units, are characterized by a discontinuous genetic divergence pattern where locally adapted and closely related genome assemblages are separated from others geographically and by significant genetic distances. Category II populations are similarly characterized by significant genetic diversity, but with weak geographic partitioning. Category III populations are the converse of II, having little genetic differentiation between assemblages that are clearly separate and likely to be reproductively isolated. Category IV assemblages have the lowest probability of being evolutionarily significant units and are characterized by extensive gene flow and no subdivision by extrinsic barriers. In addition to phylogeographic designation, the following information is used in the classification, as indicated by single-letter abbreviations: distribution (a), population response (b), phenotypic (c), and

Resumen: El stock es la unidad poblacional fundamental para los esfuerzos de conservación requeridos por ley, sin embargo, su definición formal en la literatura científica y en dos actas de conservación de los Estados Unidos es diversa y tan general que cualquier intento para usarlo en la práctica es arbitrario. Dado que la elección de los stocks merecedores de protección en su manejo es a veces un hecho políticamente contencioso, es muy importante mejorar la definición en uso.

Un elemento clave debería ser el grado en que una población puede ser considerada como una unidad evolutivamente significativa. Proponemos que se aplique un esquema jerárquico de clasificación a la designación de stocks. La Categoría I, poblaciones con la mayor probabilidad de ser unidades evolutivamente significativas, son caracterizadas por un patrón discontinuo de divergencia genética donde agrupaciones de genomas localmente adaptados e íntimamente relacionados están geográficamente aislados y separados de otros por distancias genéticas significativas. La Categoría II está también caracterizada por una significativa diversidad genética pero con una débil subdivisión geográfica. La Categoría III es la inversa de II, poseyendo una pequeña diferenciación genética entre agrupaciones que están claramente separadas y probablemente están aisladas reproductivamente. Las agrupaciones dentro de la Categoría IV, que tienen la menor probabilidad de ser unidades evolutivamente significativas, están caracterizados por un flujo génico extensivo y por una ausencia de subdivisión a través de barreras extrínsecas. Además de designaciones filogeográficas, la información usada para clasificar también

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genotypic (d) information. Included are evidence both for and against designating population as a separate stock. In the designation "Type II a/bc," for example, information to the right of the solidus would be evidence for "lumping," to the left would be for "splitting." Missing letter abbreviations would signify lack of reliable data. Note that phylogeographic designation depends on the results of selection operating to produce a locally adapted genome (indicated by differences in demographic, phenotypic, and genotypic measures) and on gene flow (indicated by differences in distribution or by movement data).

Hierarchical stock categorization allows resource managers to direct limited resources to the populations most deserving of protection, that is, the populations that are most likely to be evolutionarily significant units. Using this comprehensive classification of stock allows preliminary, conservative splitting of assemblages where data are lacking without the danger that these divisions will become entrenched as biological dogma.

Introduction

A "population stock," as defined in the Marine Mammal Protection Act of 1972 (MMPA), is a group of animals that share a common space and interbreed; a "vertebrate species," as defined in the Endangered Species Act of 1973 (ESA), is a distinct population segment that interbreeds. The purpose of such definitions in both acts is to direct management efforts to taxon levels below that of the species to ensure that populations that are uniquely adapted to given areas are not irreversibly reduced by harvest or habitat destruction. Although the stock concept is thus codified into law by these environmental acts, no useful working definitions of intraspecific taxa are provided. At the same time, no universally accepted definitions or even *pro tem* consensus exist among biologists. Thus, much confusion exists among researchers, regulators, users, and conservationists as to what taxon levels conservation efforts are to be directed toward.

The problem with the definitions of stock in the acts is that it is not obvious how to define quantitatively what is meant by either "sharing" or "interbreeding." For example, do we extend protection to the gray squirrels in Central Park in New York? They certainly meet the legislative criteria of sharing a common space and interbreeding. Or if members from two apparently distinct populations of dolphins only interbreed during EL Niño events, should these populations be managed as one management unit? What if their ranges overlap, or they interbreed once every 100 (or 1000) years? Should they then be managed as separate stocks? Of course,

debería ser incluida usando abreviaciones con letras: distribución (a), respuesta poblacional (b), información fenotípica (c), e información genotípica (d). Se incluiría tanto evidencia a favor como en contra, por ejemplo, "Tipo II a/bc" donde la información a la derecha sería evidencia en favor del "agrupamiento", información a la izquierda sería en favor de la "disociación"; la ausencia de abreviaciones con letras indicaría ausencia de datos confiables. La designación filogenética depende de los resultados de selección natural, que opera para producir un genoma localmente adaptado (indicado por diferencias en mediciones demográficas, fenotípicas, y genotípicas), y del flujo génico (indicado por diferencias en distribución o por datos sobre movimientos).

La categorización jerárquica del stock permite a los administradores de recursos asignar los limitados recursos a aquellas poblaciones que más necesitan protección, es decir a poblaciones que son, muy probablemente, unidades evolutivamente significativas. El uso de esta clasificación comprensiva de stocks permite una subdivisión preliminar conservadora de las agrupaciones cuando exista falta de datos, sin el peligro de que estas subdivisiones se transformen en dogma biológico.

there are no indisputable answers to these questions. It is absurd to apply a rigid, typological definition of stock in such situations, because at present there is no way to determine how unique and isolated a population must be before it is a "stock." Intraspecific structure theoretically can range from complete panmixia (no intraspecific structure) to isolation so complete for so long that speciation processes are at work or almost complete (Fig. 1). Rather than a universal definition that could be applied in the regulatory arena to decide if a population is or is not a "stock," what is required (and more practical) is a means of describing the usually complex biological population structure in a more informative manner.

The purposes of this paper are to show that currently used simplistic definitions of stocks are not very useful in satisfying management objectives and to suggest a way to describe population structure that captures its complexity. Using examples from the marine mammal and fishery literature, we review the history of the stock concept and methods currently used to infer stock structure. We suggest how to classify the various qualities of stocks and conclude with a case study demonstrating how the suggested method can be applied.

Background

Around the turn of the century, pioneering fishery biologists F. Heincke and J. Hjort established the local self-sustaining population as opposed to the typologically defined species as the preferred unit of study for fisher-

TWO VIEWS OF INTRA-SPECIFIC STRUCTURE

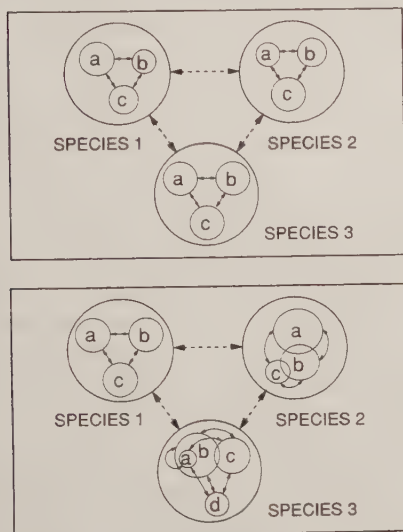


Figure 1. Two views of intraspecific structure, a "typological" and a "biological" conception of populations within species. The circles, labeled with lower-case letters, are individual populations whose geographical habitat is represented by its size and position within the species space. Where circles intersect, habitat is shared. The arrows represent exchange rates: infinitesimal between species, variable between populations within species.

In the first view, individual populations within a species are perceived as isolated, allopatric entities that can be uniquely described. Interchange between the populations, while greater than between species, is still very low, on the order of a few genomes per generation.

In the second view, the complexity and wide range of potential intraspecific structures are recognized. Habitats range from completely separate to situations where one is completely within another. Exchange rates vary between various populations, in some cases with great temporal variability due to environmental and population density changes.

ies-management questions (see Sinclair 1988; Gauldie 1991). Independently, Leopold (1933) recommended managing populations of wildlife based on their "radius of mobility," "rate of spread into unoccupied range," and "minimum units of range and population." This basic approach of managing a species at some subspecific level has therefore been a tenet in resource management for almost 100 years. In general, stock status is

conferred using a variety of proxies that imply reproductive isolation. With isolation comes genetic divergence through drift and through local adaptation via processes such as differential selection or character displacement. But because reproductive barriers within species are fragile or incomplete, especially in the marine environment, the degree of isolation of one population relative to others can be complex, varying both in space and time.

A variety of other terms in the literature all refer to organizational levels below the species: subspecies, race, deme, stock, and management unit. The use of such terms in resource management literature is highly inconsistent. Only the term "subspecies" is recognized by the International Code of Zoological Nomenclature; it is applied to populations that have received a trinomial name. The other terms, lacking such accepted usage, are frequently used to describe a variety of populations for analytical convenience or to provide status to a group because that is the most conservative approach when data are lacking and conservation issues predominate. Many so-called stocks are mere "ecological abstractions" (Sinclair 1988), and a perusal of the management literature indicates that when a term such as "stock" is used, it is used in the simplest and least restrictive sense. Little qualification is made or assumed about its genetic, evolutionary, or ecological implications. Misconceptions occur later when such stocks are expected to behave as if they were biological populations.

In 1980, an ambitious attempt to formalize the stock concept was made with an international symposium (Stock Concept International Symposium convened at Alliston, Ontario, September 29–October 9, 1980; see Booke [1981] for proceedings citation). Although many speakers emphasized the importance of management by stock, in that very large symposium only one author ventured any formal definitions. Booke (1981) defined a "phenotypic stock" as any population that maintains characteristics that are expressed depending on the environment, and a "genotypic stock" as a population maintaining Hardy-Weinberg equilibrium, that is, constant gene frequencies for a particular character in each generation. The definition of phenotypic stock is similar to a later definition by Brown et al. (1987): a population whose average life history parameters are meaningful from the standpoint of management. The definition of genotypic stock is similar to the definition of Larkin (1972), who described a stock as a population having a degree of genetic uniqueness: "a population of organisms which, sharing a common environment and participating in a common gene pool, is sufficiently discrete to warrant consideration as a self-perpetuating system which can be managed" (p. 11). Hoelzel and Dover (1989) defined a genetic stock as one that is genetically

differentiated. Presumably the genetic stock is the population that Sinclair (1988) called the "local population" in his essay on population regulation and speciation. Recently, Gaudie (1991) published a thorough review of stock concepts and their deficiencies as applied to exploited fish populations and argued for a model of populations defined on the basis of degree of interchange.

This sense of biological uniqueness via isolation is an evolutionary one, because it acknowledges the population's adaptation to local conditions and indicates that it possesses a reservoir of unique genetic variability. This is the "evolutionarily significant unit" (ESU) (Ryder 1986; see Waples 1991 for a review of its application to northwestern salmonid stocks); it is a biological population that is distinguished by its presumed evolutionary uniqueness and significance. It is a natural unit and should be a better management unit than an unnatural unit (Sinclair 1988).

Few would argue with this reasoning. In practice, however, it is difficult to define a stock based upon principles of adaptive genetic uniqueness. Existing measures of fitness are of little use in defining specific adaptation to a local environment; experimentally this is an intractable problem for higher animals. As a result, stocks are typically defined using a variety of proxies that suggest this adapted genetic uniqueness.

Stock Criteria

To study stock structure, an investigator makes observations of allopatry or isolation that imply reproductive isolation; differential life history responses, which also imply reproductive isolation; morphological (i.e., protein structures) differentiation, indicating drift or evolution under different selective regimes; or differentiation of neutral genetic characters quantifying the degree of isolation and the time since an ancestor was shared. We have categorized these sources of information as (a) distributional, (b) population response, (c) phenotypic, and (d) genetic.

Distributional Data

Initially the most important items of knowledge are those of distribution and abundance. These data pertain to all aspects of abundance, migration, pollutant and parasite loads, zones of fishery interaction and conflict, etc., that provide information about the population movements relative to geographical space and time. These data largely define whether there are major geographical barriers between putative stocks and whether they are allopatric, parapatric, or sympatric.

At the most basic level and without additional information, disjunct populations frequently have been designated as separate stocks for management purposes (e.g., Perrin et al. 1985). This is certainly a conservative

approach. Even populations that overlap for portions of their life cycle may be disjunct stocks (Iles & Sinclair 1982). Overlapping distribution does not necessarily imply gene flow; natural processes favoring adaptation to local conditions, or social selection favoring maintenance of local social behaviors, especially in the case of marine mammals, may preserve genetic differentiation in the face of apparent overlap or movements between populations (Ehrlich & Raven 1969; Slatkin 1987; Baker et al. 1990).

Presence and absence data on distribution are the most readily available sources of information on which to base stock identification decisions, but they may be misinterpreted when search effort is not continuous, causing artificial discontinuities in the reported distribution. Abundance information provides a better proxy for exchange rates. Density "troughs" or large areas of zero density indicate extrinsic barriers. Unfortunately, the variability associated with most estimates of density is such that the statistical power of using differences in density gradients in assigning stock status is often low.

Because of the importance of reproductive isolation in speciation, information on the physical movement of individuals (telemetry studies, mark-and-recapture, etc.) within their ranges brings one closer to properly assigning stock status to populations. Reeb and Avise (1990) and Avise and Ball (1990) described evidence of concordance of genetic patterns with movements for a variety of species in response to biogeographic barriers. Thus, for most populations, research on movement patterns should be given high priority.

Population Response Data

Although used frequently to distinguish putative populations, a population's life histories and behavioral traits may be modified by the environment through density-dependent control mechanisms. Data include all aspects of demography (age at sexual maturity, fecundity, growth rate, and mortality), other biological parameters, social behavior, vocalization, and specific interactions peculiar to a particular population. Behavioral characteristics are probably modified by exploitation and intra- and interspecies competition, which affect breeding site fidelity, nursing and care-giving to the young, and feeding habits, which in turn affect the pollutant and parasite loads. Still, an advantage to using population response criteria over abundance criteria should be recognized: Samples taken at one point in time when population response criteria are used integrate movement patterns over a much greater time scale than do abundance criteria.

Differences in the timing of breeding provide a particularly valuable criterion, because they imply that a barrier exists to gene flow between populations. A stock division of spotted dolphins (*Stenella attenuata*) in the

eastern tropical Pacific, for example, was originally based entirely on distribution and morphology (Perrin et al. 1979), but later was supported by differences in reproductive parameters (Barlow 1984, 1985).

Phenotypic Data

The concept of self-sustaining stocks was formulated by Heincke through his extensive examination of discontinuous geographic variation in Atlantic herring morphology (Sinclair 1988). Stocks have been defined by morphological differences of every type: color patterns, body size, shape, and skeletal characters are some examples. (Electrophoretically detectable differences in proteins are treated as genetic characters if there is evidence that such differences are inherited.) For homeotherms, morphological differences probably represent underlying genetic differences, and analyses of DNA and morphology should provide similar evidence regarding phylogenetic structuring of other groups (Sytsma 1990). The relative morphological differences between populations can be assumed to be a record of past (or present) differences in selection pressures or genetic drift. However, there are instances where morphological and molecular evidence differ due to either methodological or actual biological problems (see Box 1, Sytsma 1990). For instance, differential migration between sexes might produce strong mtDNA differences but little difference in chromosomal markers if males stray between populations and females do not. Some morphological patterns, possibly color patterns or size differences, may be ecophenotypic, that is, not stable to environmental variation. However, differences in morphological characters in mammals and birds usually yield clear information regarding population uniqueness; because the variation is assumed to be both adaptive and heritable, it is a record of past selection pressures. Given adequate sampling, morphological differences between two or more populations strongly suggest limited gene flow among these populations due either to extrinsic barriers or selection. Like the population response criteria, these types of phenotypic data integrate movement patterns over a much larger time scale than do abundance data.

Morphological differentiation has been the predominant reason for assigning stock structure to marine mammal populations. Perrin et al. (1985), for example, documented population-specific differences for spinner, spotted, and common dolphins (*Delphinus delphis*) in the eastern tropical Pacific; stock status and mortality quotas have been applied to the take of those populations by U.S. tuna purse-seiners (Anonymous 1987). Roest (1976), and more recently Wilson et al. (1990), used skull morphology to separate sea otters from Alaskan and Californian waters into separate stocks subsequently used as management units.

Genotypic Data

Booke (1981) defines a genotypic stock as a random mating population maintaining Hardy-Weinberg equilibrium; presumably, it can be defined as any random mating population that shows fixed genetic or temporally stable gene frequency differences when compared to other populations. Data include those from all studies that involve the analysis of some part of the genotype. The studies can be classified into analysis of proteins via isozyme electrophoresis or immunological techniques, molecular cytogenetics, and analysis of DNA by DNA-DNA hybridization, restriction site analysis, and sequence analysis (see Hillis & Moritz 1990 for a thorough review). The techniques involved in genetic studies and their application to marine mammals have been reviewed recently by Hoelzel and Dover (1989) and have been the subject of a recent International Whaling Commission workshop (Hoelzel 1991).

The evidence obtained from genetic methods is considered by resource managers as the most unequivocal for differentiating species and their intraspecific structure. Using genetic information for management purposes presents problems, however. Clearly it could be the ideal tool if we could directly examine the genes that constitute the locally adapted genome. One cannot do this and must rely on the analysis of "neutral" genes, primarily using allozymes and mtDNA, that are assumed to be mostly independent of selective forces. If this assumption can be made and if complete isolation is assumed, the degree of genetic divergence between two populations is a measure of the relative time since they shared a common ancestor. While we believe that significant morphological differences usually represent adaptive evolution in disparate environments, mtDNA differences between two populations may simply be a measure of time of separation. Rapid evolution through drift could accumulate significant mtDNA differences in different allopatric populations that inhabit similar environments. Still, none of these populations would presumably harbor unique adaptive genetic variability and would perhaps not warrant separate management status. In the opposite situation, lack of significant mtDNA differentiation between two populations does not necessarily mean that stocks are separate. Where barriers are "leaky," mtDNA genomes can rapidly penetrate neighboring populations independent of the adaptive chromosomal genome (Ferris et al. 1983). These "foreign" mtDNA genomes are not selectively removed from the population—they are presumably neutral. The appearance of these foreign genomes may argue for the presence of "homogenizing" gene flow and lumping the populations as one stock. In actuality, significant variation between the populations still may develop in the chromosomal genome due to differential selection pressures. As an extreme example, in Lake Victoria, 14 mor-

phological species representing 9 genera of chichlids show almost no differentiation in mtDNA sequences that are 803 base pairs in length (Meyer et al. 1990). In this case mtDNA would be a poor proxy for demonstrating differences in adaptive variation between populations.

In fact, most past genetic studies of marine mammals and other pelagic animals were not very useful for management purposes. When significant gene frequency differences between two putative populations were not found, it was easy to pass off the result as a negative one (i.e., the test was insufficiently sensitive because not enough samples or polymorphic loci were tested). And when significant gene frequency differences were detected among populations, the resource biologists have probably known from a variety of other criteria that gene flow among the groups was highly restricted. This is because considerable time and isolation were required to generate detectable differences, that is, no more than a few individuals per generation. Resource managers, however, divide populations into separate units when interchange rates are as much as several percent per year.

However, sequencing progressively longer segments of the mtDNA and nuclear genome now offers means of detecting genetic differentiation in the face of exchange rates that may be considerably higher than a few genomes per generation moving between the populations. After all, at some level, all genomes are different. So now one must ask what level of differentiation or gene flow indicates that a population has become "pan-mixed"? Deciding this requires an understanding of how much gene flow and consequent genetic diversity is "significant" or not.

Phylogeographic Taxa

Clearly, the complex interactions among movement, introgression, and selection of nuclear and cytoplasmic genomes (and the variability of expression of those genomes between local populations of a species) result in situations that are not conducive to a simplistic definition of stock or a binomial decision of stock or not-stock. Deciding whether a putative local population should be managed as a separate unit requires considerable expert biological judgment. As long as there are no means of routinely measuring the *total genetic variability of local adaptation*, rather than its proxies (distribution, population responses, phenotypic variation, or neutral genotypic variation), quasibjective decisions are necessary.

For other purposes, Avise et al. (1987; Avise 1989) devised a framework for organizing hypothetical population structures and relating the two critical concepts

of selection and movement or their products—phylogeny and distribution. They first proposed five categories but later reduced them to four (Avise 1989), two with discontinuous genetic patterns and two with continuous ones. The approach classified assemblages into one of four categories based on two criteria: mtDNA genetic distance and spatial distribution. In a recent publication, Avise and Ball (1990) characterize the interaction of both extrinsic and intrinsic reproductive barriers in the formation of subspecific divisions and emphasize the surrogate nature of most genetic and other measures (which we call proxies) of so-called stock distinctiveness.

We altered their original category criteria slightly to be more general and to emphasize that meaningful distinctiveness must come from the expression of multiple, independent genetically based traits (Avise & Ball, 1990). *In our alteration, the horizontal axis indicates the degree of response to differential selection likely to have occurred in one population relative to another.* It represents differences in characters that are the expression of the locally adapted genome, rather than simply the mtDNA genetic distance (Fig. 2). Under this scheme, differences found in demographic, morphological, isozyme, or mtDNA measures are taken to be proxies indicating that selection may be operating differentially

Theoretical classification:

		PHYLOGEOGRAPHIC TYPES	
GENE FLOW	little or none	III	I
	high	IV	II
		little	great
		DIFFERENTIAL SELECTION	

Operational classification:

		PHYLOGEOGRAPHIC TYPES	
GEOGRAPHIC LOCALIZATION	great	III	I
	little or none	IV	II
		little	great
		PROXIES for DIFFERENTIAL SELECTION	

Figure 2. Four phylogeographic classification categories. The horizontal axes in the theoretical classification refer to differences in the characters expressed by the genes that make up the locally adapted genome. The horizontal axis in the operational classification refers to differences in characters that may or may not be expressed by the genes that make up the locally adapted genome. If they are not expressed, the differences represent proxy measurements indicating the probability that sufficient time has elapsed and selection pressure has been applied so that a locally adapted genome has evolved. Gene flow is defined as production of locally fit offspring. Adapted from Avise (1989).

on one population relative to another. Measures on this axis mostly represent the culmination of selection operating on many generations.

The proxy for gene flow, distribution difference, is the other axis of the matrix. It is considered separately to emphasize that available information usually only indicates potential gene flow. Actual flow of genes requires the production of fit offspring. The advantage of looking at populations in this way is that a matrix of four population relationships can be *operationally* described. It is a hierarchical organization because with each step there is an increasing *probability* of the population in question being an ESU (Phylogeographic categories I through IV; Fig. 2). Note that a stock is always characterized as a "population" in relation to another reference population. The proposed system works as follows:

Category I Populations

The easiest situation to deal with is that of allopatric populations demonstrating significant genetic differences; there would be little argument that these should be managed as separate units. Category I is characterized by a discontinuous genetic divergence pattern where locally adapted and closely related genome assemblages are separated from others geographically and by significant genetic distances—great genetic divergence/strong geographic partitioning. This could have been caused by long-term, extrinsic barriers (zoogeographic) or by extinction of intermediate assemblages in cases with limited gene flow.

Category I situations are characterized by the presence of actual geographical separation by physical barriers such as land masses, or oceanographic or topographical barriers such as temperature clines, etc., which effectively create a margin around a population. Genetic and other differences from populations elsewhere are implied but are not necessarily proven. The population is effectively isolated and probably is never confused with another in management programs.

Category II Populations

Category II is characterized by a discontinuous genetic diversity pattern between groups of closely related genome assemblages existing sympatrically or parapatrically—that is, great genetic divergence accompanied by weak geographic partitioning. Avise et al. (1987) speculate that this may have arisen through allopatric divergence and secondary contact or through some intrinsic (reproductive) barriers.

This requires that two (or more) populations/putative stocks coexist with total sympatry or with extensive geographical overlap or be weakly defined in parapatry. Geographically there would appear to be no reason not

to manage them together, but critical differences in behavior, morphology, genetics, or some combination of these indicate reproductive isolation to some degree. This type of stock is perhaps the most critical and difficult to manage.

Avise et al. (1987) and Avise (1989) find no good examples of this category and report that it is rare to find mtDNA differences greater than 1 to 2% between individuals collected from the same locality. Using mtDNA divergence measurements, Hoelzel (1991) reports considerable genetic isolation between at least partially sympatric populations of killer whales (*Orca orcinus*) off Vancouver Island; they suggest that these groups represent a category II population structure. They are not category I (or III) populations because of their at least partially sympatric distribution and potential for genetic interchange.

Category III Populations

The remaining two categories are characterized by a pattern of continuous genetic divergence. Category III parallels category I; however, here the geographically separated assemblages are characterized by little genetic differentiation, for instance, less than 1% for mtDNA diversity. Still, the populations are clearly separate, either because of true allopatry or strict parapatry, and there is a high degree of reproductive isolation, as evidenced by various combinations of demographic and morphological differences, although there are no barriers to intermingling at the margins and interbreeding is feasible. There may or may not be various combinations of demographic, morphological, and genetic differences. In any case, geographically concordant unique genome assemblages have developed within local habitats in response to local selection pressures.

Category IV Populations

Category IV populations have extensive gene interchange and no subdivision by geographic barriers. Populations in this category appear panmictic and occupy a broad range that blends with that of neighboring population(s) rather than abutting on them. There are usually minimal, if any, differences in morphology, genetics, and demographic parameters between them, and the main distinguishing feature indicating that this is a separate population is that the center of abundance may be some distance from the center of neighbors. There is little or no reproductive isolation, and there is considerable intermingling on the breeding grounds. This category typifies the most nebulous classification and may show poor evidence for any stock differentiation. Depending on the management issue, certain geographical regions occupied by such populations may still be treated as separate stocks for the sake of conservatism.

Qualified Phylogeographic Taxa

The manner in which such a phylogeographic classification of any given population is made and the confidence in such a decision depends on the amount of information available. We suggest that this information be appended to the phylogeographic taxa using a shorthand method (Fig. 3). A shorthand notation is necessary because resource management documents usually contain extensive lists of stocks that have received or are being considered for separate management status. Using this approach, reference to a given management unit would carry with it information regarding its phylogeographic structure (category type) and the data from which the decision was made (criteria basis).

The phylogeographic category is designated by a Roman numeral (I, II, III, and IV; Fig. 2). The proxy information with which decisions regarding the population are made is designated as "a" (distribution and movement), "b" (population responses), "c" (phenotypic differences), and "d" (genotypic differences). A population would be designated by phylogeographic category and decision criteria, for example, II a/bcd. Letters to the left of the solidus represent data for "lumping" and those to the right, data for "splitting" the group (Fig. 3).

A population that has a high probability of being an ESU is immediately apparent from its phylogeographic category. The degree of confidence in such a classification is indicated from the type of information that was marshalled to make the decision. Situations where information was lacking or equivocal could be informative from a management sense. In cases where information regarding one or more of the criteria was unavailable, the letter designation would not be present (perhaps a dash could be substituted), or the same letter could appear on both sides of the solidus if information was equivocal or unresolvably contradictory. A stock designation of type III c/ad would probably stimulate more

aggressive management than one designated as III c/a, and such a designation would help focus additional research efforts. Where there is clear geographic separation but extensive overlap of margins temporally, as in type III, we might wish to denote this fact by indicating the stock as III a/a. In another example, where population response is to be included in the stock criteria, there might be no difference between demographic parameters and pollutant and parasite loads, but clear differentiation between dialects. The stock that perhaps might be type II might then be designated as II b/b. If all aspects showed clear differences, then the category would be II /b.

In the appendix, we have chosen a marine mammal species to illustrate the procedure. The minke whale (*Balaenoptera acutorostrata*) has populations with relationships demonstrating each of the four phylogeographic categories. Current biological information on the minke whale is provided in detail, covering as much ground as possible under each of the four criteria. Classifications are suggested for the various putative stocks.

The Decision Process

This proposed system of phylogeographic classification of course addresses only single-species considerations. Because of ecological phenomena such as predator-prey interactions, the existence of keystone species and species guilds, etc., a population may be important beyond its qualifications, or lack thereof, as an ESU; these factors must also be considered in deciding what should comprise a management unit.

It is most important that the phylogenetic classification be carried out as an exercise separate from and prior to consideration of the socioeconomic and political factors that inevitably influence the management status of a population, and, further, potential conflicts of

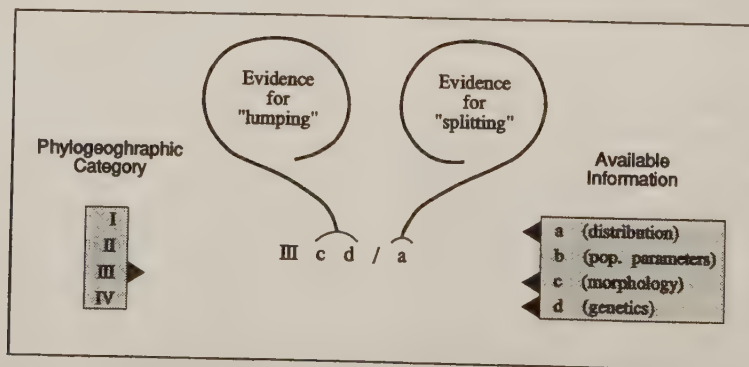


Figure 3. A shorthand method for qualifying stock type using phylogeographic categories and information regarding the criteria used to make such qualifications.

interest should be carefully weighed and considered in selecting an expert or panel of experts to make the classification. Ideally, populations should be surveyed and phylogeographically classified *before* situations demanding management decisions arise.

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Appendix

In the earlier part of this paper, we endeavored to show how stocks may be classified, with the aid of some guidelines, into one of four major categories. Information that describes characteristics of populations may then be added as qualifiers to include (a) distribution, (b) population response (demographic or behavioral), (c) phenotypic information (morphologic), and (d) genotypic information (Fig. 3). Arguments for classification must be made in the knowledge that information is constantly being updated and that intraspecific populations themselves are dynamic and therefore subject to change over time and in response to new information. Our attempts at classifications are thus open to testing both now and in the future.

Minke Whale

Balaenoptera acutorostrata

I. Taxonomy

A. Subspecies—*bonaerensis*

B. Morphs

1. Davidsoni-type
2. Bonaerensis-type
3. Dwarf

II. Provisional management units*

A. Southern Hemisphere—six management areas defined by longitude from the equator to ice edge

1. Area I, 120°W–60°W
2. Area II, 60°W–0°
3. Area III, 0°–70°E
4. Area IV, 70°E–130°E
5. Area V, 130°E–170°W
6. Area VI, 170°W–120°W

B. Northern Hemisphere—two main populations, one smaller

1. North Atlantic
 - a. Canadian east coast
 - b. Central

c. West Greenland

d. Northeastern

2. North Pacific

a. Okhotsk Sea—Western Pacific

b. Sea of Japan—Yellow Sea/East China Sea

c. East Okhotsk Sea—Western Pacific

3. Northern Indian Ocean

III. Evidence

A. Distribution

1. Range

Distribution is global, but there is no evidence from tagging, abundance, etc., that Northern and Southern Hemisphere populations mingle at any time, even though the equator may be breached in some regions, for example, off Brazil. The pattern of latitudinal seasonal migration associated with feeding (in polar waters) and breeding (in warm low latitudes) effectively isolates the populations of the two hemispheres, which are out of phase by 6 months. However, there is a possibility, yet to be proved, for interchange in some marginal equatorial regions where temporarily segregated portions of the population such as mature females or males may reside almost year-round. Latitudinal segregation of different portions of the population by sex, age, and reproductive status are well documented (Wada 1989).

Tag return data suggest mixing longitudinally at the boundaries (as defined above) between southern stocks (Wada 1984). There is evidence for interchange between Areas IV and V, for example. The region of occupation of the dwarf form in the southern oceans is longitudinally wide (Southwest and Southeast Atlantic, Southwest Pacific), but it is perhaps excluded from high latitudes (Best 1985; Arnold et al. 1987).

In the Northern Hemisphere, stocks have been defined mainly in response to national and regional exploitation patterns and to a large extent were originally not biologically based. Tag experiments do not link West Greenland animals with the eastern Atlantic ones, and they appear to be separate. The species is highly migratory, and movements of several thousands of kilometers, even within a few days, are well documented in latitudinal direction (Horwood 1990). Unless there are actual or partial geographic, oceanographic, or other barriers to east-west excursions, the whales from the various regions must be considered to probably intermingle.

The relationships of the minke whales in the southern and northern Indian Ocean are not known, although populations exist on each side of the equator. The southern animals clearly occur in and around Areas III and IV. In the northern region, animals are observed year-round in the Red Sea, Gulf of Aden, Persian Gulf, and the seas surrounding Sri Lanka and Indonesia (Horwood 1990).

2. Contaminants

Tanabe et al. (1986) reported concentrations of PCBs (0.0031–0.029 ppm wet weight) and DDEs (0.013–0.14

* Populations and stocks as defined by the IWC—International Convention for the Regulation of Whaling, 1946, Schedule October 1989.

ppm wet weight) in blubber of Antarctic Area IV and V minke whales to be mostly lower than those observed for the Northern Hemisphere, where levels are 0.14–1.1 ppm wet weight for PCBs and 0.21–2.6 ppm DDT off West Greenland (Johansen et al. 1980), and 27.45 ppm PCBs and 1.09 ppm DDT in the St. Lawrence estuary, Canada (Sergeant 1980). The differences are clearly due to feeding ground separation, and show clear distinctions between the hemispheres.

3. Parasites

Comparison of infestation rates of ectoparasites in adjacent Antarctic Areas I, II, and III (Bushuev 1986, 1988) suggest that differences exist between populations. In Area III, 34–57% of the whales are infested, compared with 2–11% in Area II (with variable incidence from east to west) and almost zero infestation in Area I. Ohsumi et al. (1970) reported very low ectoparasite infestation in Area IV, and later investigation over 3 years showed significant differences between Areas I, III, and IV. The differences were interpreted as indicating that stocks are separated on the feeding grounds.

B. Population response

The Southern Hemisphere minke whales have been documented to respond indirectly to exploitation of competitor species in a density-dependent manner, with consequent reduction in the age at sexual maturation from about 12–13 years to 7–8 years during a 30-year period (Area III) (Kato 1987). Masaki (1978, 1979), Kato (1983), Kato et al. (1984), and Ohsumi (1986) reported similar changes in age at sexual maturation for Areas III and IV combined. The pattern of trends and values of biological parameters seems similar for the Areas, but perhaps the response has been greatest in the most heavily exploited Areas, I, II, and III (Horwood 1990).

Rather less is known for the Northern Hemisphere because of difficulties in age determination. Still, sexual maturation is reported to be about 7.3 years in the North Atlantic.

C. Phenotypic Data

The Northern and Southern Hemisphere forms of the minke whale are different in coloration (flippers, baleen, etc.) size, and skeletal morphology, the southern form being designated as the *bonaerensis* form. With the exception of the newly described dwarf form, mature animals from the southern population are generally larger than those from the northern populations (Lockyer 1984). The Atlantic minke is also slightly larger than the Pacific minke.

In the Southern Hemisphere, two morphological types were traditionally reported, one with plainly pigmented flippers and the other with asymmetrical two-tone coloration; both belong to the *bonaerensis* form (Williamson 1959; Ohsumi et al. 1970; Taylor 1957; Aguayo 1974; Baker 1983; Gaskin 1972; Kasuya & Ichi-

hara 1965). Currently, there are three reported color forms of minke whale, mainly defined on the basis of extent and symmetry (left and right sides) of flipper coloration—the presence, absence, or intermediary of a white band, the extent of pale coloration of the baleen, and dark pigmentation around the neck and throat region (Best 1985). The new evidence for a diminutive or dwarf form in the southern oceans, mainly reported from South Africa, Australia, New Zealand, and Brazil (Best 1985), is largely based on the definition of a third color morph characterized by symmetry of coloration and white flippers. In addition, the third form is consistently smaller. Best (1985) concluded that the dwarf form was also sufficiently different in skull characters from the southern *bonaerensis* subspecies that it was at least as distinct as the northern *davidsoni* form from the *bonaerensis* one.

D. Genotypic Data

Restriction fragment analyses using 14 restriction enzymes of minke whale mtDNA D-loop from four populations—Antarctic Areas IV and V, *bonaerensis* type, Antarctic Area IV dwarf form, Sea of Japan and western North Pacific (*davidsoni* type)—indicated 4–11% genetic nucleotide diversity (Wada et al. 1991). In Areas IV and V (*bonaerensis* form) the genetic diversity within populations is only 0.17%, compared with 0.05% within the western North Pacific and 0.00% within the Sea of Japan. Nucleotide diversity shows no significant differences between Areas IV and V, but significant differences between the *bonaerensis*, dwarf, and *davidsoni* forms, the latter two being relatively more closely related, with genetic diversity of about 4% (Fig. 4).

The diversity between the Sea of Japan and the western North Pacific is only 0.06%, but is >10% between Northern and Southern Hemisphere minke populations. Wada and Numachi (1991) presented results of enzyme electrophoresis on tissue proteins from different baleenopterid whales that indicated that genetic differentiation between Antarctic and western North Pacific Sea of Japan and Korean stocks was about seven times

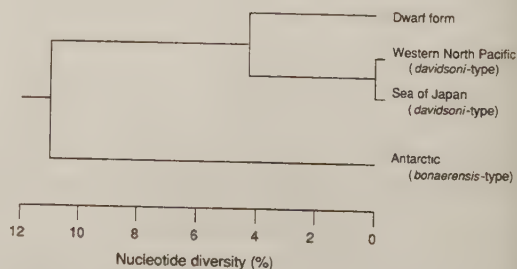


Figure 4. mtDNA sequence divergence among four minke whale samples. After Wada et al. (1991).

greater ($D = 0.0826$) than that within the North Pacific, to the extent that the differences were far greater than those between the separate sibling species *B. borealis* (sei) and *B. bryde* (Bryde's). This suggested that northern and southern minke were separate species, or at least separate subspecies.

DNA nuclear probes suggest significant differences between the Antarctic, North Atlantic (West Greenland), and the western North Pacific (Sea of Japan) populations (Amos & Dover 1991). The results could be translated into migration rates between regions. The high level of migration between adjacent Areas IV and V was enough to make separate stock identity questionable (Hoelzel & Dover 1991).

In the North Atlantic, Palsboll (1990) reported on restriction fragment analysis of ribosomal DNA of minke from the Northeastern Atlantic (Barents Sea) and West Greenland. He found that there was a probability of less than 0.001 that the two stocks were from a single random-mating population—good reason for identifying the stocks as separate. Arnason and Spilliaert (1990) reported evidence of stock differences between minke from the Norway (Northeastern stock—Barents Sea), Iceland (Central stock), and West Greenland. Using genomic DNA probes, they found the greatest differences between West Greenland and the others. Differences were also found between Iceland and the Barents Sea populations. They concluded that existing management stock divisions were valid. Danielsdottir et al. (1990) also found supporting evidence using electrophoretic analyses on the separation of these three stocks. Using restriction fragment analysis of mtDNA, however, Palsboll (1990) found conflicting and contradictory results for these three regions. Bakke and El-Gewely (1990) reported stock differences between northern Norway and the west coast of Svalbard using the same techniques.

IV. Classification

The minke whale has been comparatively well investigated and defined in terms of stock identity, probably because the species has been exploited on an international scale. The evidence seems strong that the Northern and Southern Hemisphere populations are clearly distinct and in category I b/abcd status, and the subspecies category seems valid. The North Atlantic and North Pacific stocks also appear distinct and in category I status.

In the Southern Hemisphere, clearly it seems that populations in Areas III, IV, and V are not easily discernable and probably should be afforded category IV abcd/a status—very weak stock definition, if any. However, compared to the southern *bonaerensis* subspecies, the dwarf form also could be afforded subspecies status, but it would be ascribed to category II because of sympatric distribution. The final categorization might be II a/cd.

The North Atlantic stock definitions appear to be largely supported by genetic analyses, and the majority when compared would be given category III c/acd status.

This species is of particular interest in stock analysis because of multiple representations in each stock category, I–IV. The recent genetic investigations have brought to light the fact that speciation, not just subspeciation, may be occurring in the minke whale populations. In the future, the whole question of what constitutes a species may have to be reconsidered for the family Balaenopteridae.

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Abstract. – The basis for the curious association between yellowfin tuna *Thunnus albacares* and spotted dolphin *Stenella attenuata* in the eastern tropical Pacific Ocean has never been explained. Consideration of the bioenergetics of the associated tuna and dolphins suggests that the association may be based on the combined effects of a shallow thermocline, overlapping size (length) ranges of associated yellowfin and young dolphins, congruent diets, hydrodynamic constraints on swimming speeds of dolphin schools, and social (care-giving) behavior of dolphins. Insights developed during construction and exercise of comparative bioenergetics models for the tuna and dolphin suggest that tunas are more likely to follow dolphins than dolphins to follow tunas, and that the strength of the association in a given area may be related to oceanographic conditions affecting prey distribution and abundance.

Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: A basis for the bond

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In the eastern tropical Pacific Ocean, yellowfin tuna *Thunnus albacares* and spotted dolphin *Stenella attenuata* form an association strong enough that the fish can be captured by capturing the associated dolphins (e.g., Orbach 1977). The dolphins, easier to locate than the tuna, form the sighting cue for locating tuna schools. Despite chases lasting on average about half an hour (and occasionally as long as 2–3 hours) the fish tend to remain with the dolphins throughout. Eventually the dolphins tire and can be encircled, along with the associated tunas, with a purse-seine net.

Although the subject of substantial conjecture (e.g., Perrin 1969, Orbach 1977, Au and Pitman 1986, Au 1991), no definitive explanation exists for the association, perhaps in part because conjectures to date have been qualitative rather than explicitly quantitative. Quantifying the advantages or disadvantages of the association in terms of the energetics of its component groups holds promise for helping understand the bond, because such quantification can more readily expose conceptual errors, lead to unexpected insights, and form the basis for testable hypotheses. Expressing relationships in terms of energy flow (e.g., cost of finding food, cost of reproduction, feeding requirements, etc.) has often proved a useful format for developing understanding of biological phenomena. Following this precedent, I present here bioenergetics models for both tunas and dolphins in a “typical”

association in the eastern tropical Pacific Ocean. I use these models to estimate feeding rates of tuna and dolphins, and discuss implications concerning the ecological advantage to tuna (or dolphins) when associated with dolphins (or tuna).

Estimates of forage requirements predict that tuna and dolphins should experience severe competition under some circumstances of prey distribution and abundance, but perhaps not under others. Observations of overlaps in sizes between associated tuna and dolphins and of morphological similarities between the animals have implications for the importance of swimming energetics to the association.

These estimated forage requirements and considerations about swimming energetics are discussed in terms of their implications for determining which component (tuna or dolphins) controls the association, how the competition might be mitigated, when the association might be more likely to occur, and how these factors might be used to locate large yellowfin tuna unassociated with dolphins. The last point is important in relation to current interest in eliminating the practice of “dolphin-fishing” in the eastern tropical Pacific Ocean. “Dolphin-fishing” involves location and capture of tuna schools by locating and capturing associated dolphin schools; as air-breathers, the dolphins are more easily sighted than the tuna due to the dolphin’s surface activity. Other explanations for the bond, and poten-

tial conflicting evidence, are discussed briefly as they relate to the energetics models and results presented here.

Methods: Model development and description

The tuna-dolphin association

The tuna-dolphin association occurs in the eastern tropical Pacific Ocean (ETP) in a triangular region roughly the size of the continental United States (~ 10 million km^2), extending along the western coast of the Americas from the tip of Baja California ($\sim 20^\circ\text{N}$) south to Peru ($\sim 20^\circ\text{S}$) and seaward to $\sim 140^\circ\text{W}$ (Fig. 1). Total productivity in this area tends to be low relative to all other oceans, but high relative to other tropical oceans. Ocean currents and winds generate a typical pelagic environment in which areas of high productivity are distributed in dynamic, nonrandom, complex patterns (Fiedler et al. 1990, Fiedler 1992).

The ETP is characterized by an exceptionally shallow surface mixed layer. In contrast to other areas of the equatorial Pacific where the thermocline is generally 150–200 m deep (Kessler 1990), the depth of the thermocline layer throughout much of the ETP extends only 50–100 m below the surface (Fig. 1). Water temperatures in this wind-mixed layer are quite warm (25 – 30°C) and oxygen concentrations are high (Wyrtki 1966 and 1967, Fiedler et al. 1990, Fiedler 1992). Below this layer, water temperatures fall relatively rapidly (from ~ 27 to $\sim 15^\circ\text{C}$) through the thermocline (usually 5–25 m vertical extent), stabilizing again below the thermocline (Fiedler et al. 1990). Oxygen concentrations also decrease relatively rapidly through the thermocline, increasing again in cold water at greater depths.

Strong dependence on warm water and on high concentrations of oxygen apparently force both tuna and dolphins into this unusually shallow mixed layer. Tuna must swim more or less constantly both to provide an adequate flow of sufficiently-oxygenated water over their gills and to locate adequate food supplies (e.g., Magnuson 1978, Olson and Boggs 1986). Yellowfin tuna would likely have difficulty maintaining an adequate energy balance swimming in the colder waters below the mixed layer, nor can they afford being caught for long in the oxygen minima characteristic of the thermocline.

Dolphins are constrained to reside near the ocean surface in order to breathe. Only temporary excursions below the mixed layer are tolerable, both because of this requirement for gaseous oxygen and because the blubber layer of the tropical dolphins involved in the tuna-dolphin association is too thin to maintain thermo-

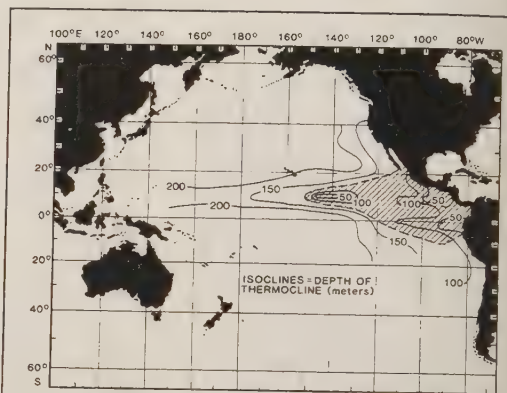


Figure 1

Depth of mixed layer in the area of the eastern tropical Pacific Ocean characterized by associations between yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata*. Tuna-dolphin fishery occurs roughly in area delimited by the 300 m isocline.

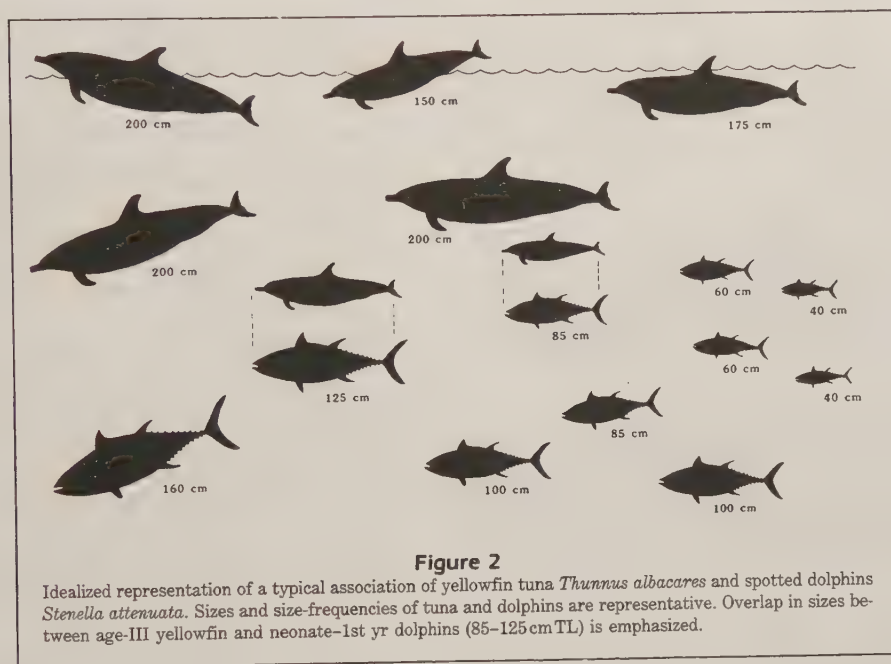
neutrality in waters much colder than that in the mixed layer (unpubl. estimates). This is not necessarily a disadvantage, as the major prey for associated tuna and dolphins (small fish and squid; Perrin et al. 1973) also tend to concentrate in this upper mixed layer, at least periodically throughout a 24-hour day.

Although any individual tuna-dolphin association is doubtless dynamic in the details of its spatial configurations and component individuals, the association in general can be envisioned as a loose aggregation of animals characterized by dolphins swimming relatively near the ocean surface, separated vertically from the tuna swimming below by only a few meters (Fig. 2).

Although several species of dolphins and two species of tuna have been found to associate in the ETP, one species of dolphin (spotted dolphin *Stenella attenuata*) and one species of tuna (yellowfin *Thunnus albacares*) comprise the majority ($>80\%$) of the associations (e.g., Orbach 1977, IATTC 1989). The remainder of this paper assumes the "tuna-dolphin association" includes only these two groups.

Energetics models

Both models followed the same format, using the standard bioenergetics approach of balancing food requirements against estimated energy costs for metabolism and energy savings as growth in biomass (University of Wisconsin Sea Grant 1989). The Wisconsin bioenergetics model derives estimates of consumption by



iteratively fitting an energetics equation for growth in body weight over time, to observed growth-rate curves derived from field samples of the organism in question. When the model growth curve simulates well the observed growth curve, the other fluxes estimated by the model are presumed to be reasonably accurate.

Specific rates (calories of flux · calories of animal⁻¹ · day⁻¹) of energy flux were estimated based on data derived from various sources for individual tunas and dolphins as a function of size. Rates of energy flux for schools of dolphins and tuna were estimated as the sum of weight-specific estimates for individuals in each group.

Costs of reproduction were ignored for both yellowfin and spotted dolphins; in the yellowfin model because the model focuses on the sizes of yellowfin associated with dolphins, which tend to be relatively immature fish. Spawning activity in yellowfin does not occur in fish much smaller than 80 cm, and increases slowly to the maximum activity in fish larger than ~150 cm (Joseph 1963). Energy costs of reproduction for spotted dolphins were omitted because the fraction of pregnant, lactating, or pregnant and lactating females in a typical school at any time is relatively small (~25%; see School composition).

Some of the energetics parameters reported here for spotted dolphins are based on morphological measure-

ments from 4 dolphin specimens from the ETP; 3 spotted dolphins measuring 81–189 cm total length (TL), plus 1 spinner dolphin *Stenella longirostris* 114 cm in length. The 81 cm individual was a very late-term fetus carried by the 189 cm animal. Although this sample is very small, all morphological measurements from these 4 animals fall well within the bounds of size-related regressions of morphological characteristics derived subsequently for a sample of 34 spotted dolphins measuring 74–215 cm TL (tip of rostrum to fluke notch) (unpubl. data).

School composition The yellowfin model addresses only those sizes of yellowfin found associated with dolphins (relatively large age-II and age-III fish, 55–125 cm TL; Fig. 3). Based on catch records from the fishery, an "average" association was assumed to include 500 yellowfin with an age composition of 65% age-II and 35% age-III fish per school (Ashley Mullin, IATTC, c/o Scripps Inst. Oceanogr., La Jolla; unpubl. data from commercial fishery).

Dolphin school composition was assumed to reflect the apparent age distribution of the spotted dolphin population, which in turn was assumed to appear as the length (age) distribution of dolphins collected during purse-seining operations in the ETP (Smith 1979, Barlow and Hohn 1984; A. Hohn, NMFS Southwest

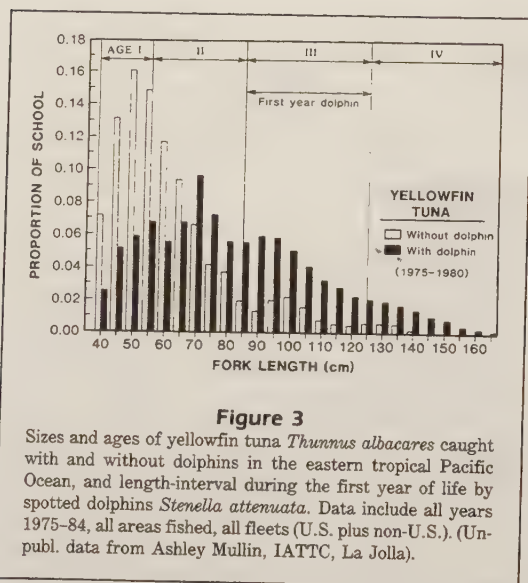


Figure 3

Sizes and ages of yellowfin tuna *Thunnus albacares* caught with and without dolphins in the eastern tropical Pacific Ocean, and length-interval during the first year of life by spotted dolphins *Stenella attenuata*. Data include all years 1975-84, all areas fished, all fleets (U.S. plus non-U.S.). (Unpubl. data from Ashley Mullin, IATTC, La Jolla).

Fish. Sci. Cent., La Jolla, unpubl. data). Proportions of nursing calves (ages 0-2 yr), adolescents (ages 3-14 yr), sexually adult males (ages 15 and up), and sexually adult females (ages 11 and up) in an average school were 0.05, 0.40, 0.25, and 0.30, respectively. Proportions of adult females not pregnant or lactating, lactating, pregnant, and pregnant and lactating animals were 0.05, 0.15, 0.08, and 0.02, respectively.

Weight-length conversions The tuna model used, as the calibration growth curve, the Gompertz fit derived by Wild (1986) for yellowfin tuna from the ETP. When necessary, body fork lengths in centimeters (cmFL) were converted to wet weights in grams (WW_g) using the length-weight relationship (Alex Wild, IATTC, La Jolla, unpubl. data for yellowfin tuna from the ETP)

$$FL = e^{((\ln(WW_g/1000) + 11.184)/3.08612)}$$

The calibration growth curve for expected size-at-age in spotted dolphins was derived from equations and figures in Hohn and Hammond (1985) and unpublished data (A. Hohn, Southwest Fish. Sci. Cent., La Jolla). Weight-length conversions assumed the relationship

$$WW_{kg} = 1.4 \cdot 10^{-5} \cdot TL^{2.95}$$

where WW_{kg} is wet weight in kilograms, and TL is total length (tip of rostrum to fluke notch) in centi-

meters, based on weight-length measurements from a sample of 50 spotted dolphins ranging in size from 82 to 210 cm TL.

Equations Each model included equations for specific rates of consumption (C_{sp}), respiration (R_{sp}), including both swimming activity ACT_{sp} , and standard metabolism STD_{sp} , heat of digestion (specific dynamic action, SDA_{sp}), and waste losses (excretion plus egestion; WL_{sp}). Specific rate of growth is estimated simply as the difference between consumption and the sum of energy expenditures.

The form of the equation for each specific rate was the same for both models, with the exception of R_{sp} , which was estimated for yellowfin using Boggs' (1984) experimental results. R_{sp} was estimated for dolphins following Magnuson's (1978) procedure for estimating cost of swimming by carangiforms.

No effect of water temperature on consumption or respiration rates appears in either model. Ambient water temperature was assumed to be constant at 27°C, as most of the tuna-dolphin habitat occurs in waters of this temperature.

Consumption Specific rate of consumption (C_{sp} ; calories food consumed · calories of animal⁻¹ · day⁻¹) was estimated as

$$C_{sp} = \text{CONS}_{cal} / \text{CAL}_{an}$$

CAL_{an} is total caloric content of an individual yellowfin or spotted dolphin, estimated as a function of wet weight in grams,

$$\text{CAL}_{an} = \text{CD} \cdot \text{WW}_g$$

where CD is caloric density (cal/g wet wt) of yellowfin tuna¹ or spotted dolphins².

CONS_{cal} is total calories consumed per individual per day, estimated as

$$\text{CONS}_{cal} = \text{CONS}_{ind} \cdot \text{CD}_f$$

where CD_f is caloric density of food (cal/g wet wt) for

¹ 1440 cal/g wet wt (Boggs 1984).

² $\text{CD}_d = 1860$ cal/g wet wt; average caloric density of four dolphins measuring 81-189 cm TL. Caloric density of each animal was determined as the sum of calories contained in blubber, muscle, viscera, and bone divided by total animal wet weight in grams. Average caloric density of individual dolphins ranged from 1985 cal/g wet wt in the 81 cm animal, to 1760 cal/g wet wt in the large adult female (189 cm TL). Assuming constant energy density for spotted dolphins is acceptable, as spotted dolphins do not appear to exhibit any significant seasonal, and little age-related, changes in thickness of their blubber layer.

yellowfin tuna³ or spotted dolphins⁴, and $CONS_{ind}$ is wet weight in grams of food consumed, estimated as

$$CONS_{ind} = C_{max} * P_{val} * WW_g,$$

where C_{max} is maximum possible consumption (expressed as a fraction of wet weight) for the largest yellowfin or dolphin, estimated as

$$C_{max} = C_a * WW_g^{C_b},$$

where ${}^5C_a = 1.2$ and ${}^6C_b = -0.22$ for yellowfin, or ${}^7C_a = 3.98$ and ${}^8C_b = -0.29$ for spotted dolphins.

P_{val} is an iteratively fitted unitless value in the range 0–1 that, when “correct,” results in the simulated growth curve matching the observed growth curve (University of Wisconsin Sea Grant 1989), and WW_g is body wet weight in grams.

Respiration (yellowfin tuna) Specific rate of respiration (R_{sp} ; calories respired · calories of animal⁻¹ · day⁻¹) for yellowfin tuna was estimated as

$$R_{sp} = (STD_w + ACT_w) * (20650/CD),$$

with energy costs of standard (STD_w) and active (ACT_w) metabolism expressed in watts. The factor

³Energy density of yellowfin food was based on an assumed diet of 70% fish, 20% squid, and 10% invertebrates (Olson and Boggs 1986), with undigestible fractions of 0.124, 0.066, and 0.025, and caloric densities of 1440, 1260, and 1000 cal/g wet wt, respectively. Average ingested energy density (including the undigestible fraction) is 1380 cal/g wet wt.

⁴Energy density of spotted dolphin food changes with age (size). Spotted dolphins nurse throughout their first year (Perrin et al. 1976). They do not begin to ingest solid food until their second year, and they do not stop nursing entirely until their third year when they are ~145 cm in length. In this simulation, dolphins up to 1 yr of age were assumed to consume only milk (2855 cal/g wet wt) (Pilson and Walker 1970). Diet during the second year was assumed to be the same as that for yellowfin tunas, with an ingested energy density (CD_i) of 1380 cal/g wet wt.

⁵Based on the assumption that maximum specific feeding rate for very large yellowfin tunas (95000 g wet wt) would not exceed 10%/day, then solving for the intercept C_a (i.e., $C_a = 0.10/(95000^{-0.22})$) yields $C_a = 1.2$. In practice, the exact value chosen for C_{max} is flexible, as higher values simply reduce the fitted value of P_{val} , and vice versa.

⁶By analogy to walleye *Stizostedion vitreum* (Kitchell et al. 1977).

⁷Assuming maximum possible ration for adult spotted dolphins (~75 kg) would not exceed 15% of body weight/day (Sergeant 1969), and with $C_{max} = 0.15$, $WW_g = 85000$ g, and $C_b = -0.29$, then $C_a = 3.98$.

⁸As a compromise between the unresolved arguments of Kleiber (1961; $C_b = -0.25$) and Heusner (1982; $C_b = -0.33$) for scaling of metabolic rate with size in mammals. This compromise was chosen because consumption is not strictly a metabolic rate. While Huesner's argument for metabolic rate is supported by data for metabolic rate changes with size (see formulation for dolphin respiration), no such data exist for consumption rates.

20650 converts watts to cal/day. Dividing by caloric density of the animal (CD) produces the specific rate.

Weight-specific energy cost of standard metabolism for yellowfin was assumed constant for all sizes of yellowfin (Boggs 1984) as

$$STD_w = 0.464 \text{ watts/g wet weight.}$$

Energy cost of active metabolism (watts/g wet wt) was estimated using Boggs' (1984) equations and data for energy costs of activity in yellowfin,

$$ACT_w = F * VL^G * FL^H,$$

where VL is velocity in cm/sec and $F (= 1.59 \text{ E}^{-4})$, $G (= 1.64)$, and $H (= -1.28)$ are fitted parameters derived from Boggs' (1984) laboratory studies on yellowfin energetics.

Yellowfin were assumed to swim at length-specific optimum-sustained cruising speeds, with velocity scaling to fish length as

$$VL = VL_a * FL^{VL_b},$$

where ${}^9VL_a = 20.6$, and ${}^{10}VL_b = 0.4$.

Respiration (spotted dolphins) Specific rate of respiration (R_{sp} ; calories respired · calories of animal⁻¹ · day⁻¹) for spotted dolphins was estimated as

$$R_{sp} = (ACT_{sp} + STD_{sp} + HL_{rsp}),$$

where ACT_{sp} is specific rate of swimming activity, STD_{sp} is specific rate of standard (basal) metabolism, and HL_{rsp} is specific rate of residual heat loss.

Specific rates of swimming activity and standard metabolism are estimated as

$$ACT_{sp} = ACT_{cal}/CAL_{an}$$

and

$$STD_{sp} = STD_{cal}/CAL_{an}.$$

Caloric cost of standard metabolism was estimated as

$$STD_{cal} = S_a * WW_g^{S_b},$$

⁹Intercept estimate based on 100 cm FL yellowfin swimming on average 130 cm/sec *in situ* (Holland et al. 1990).

¹⁰Slope estimate based on theoretical and empirical studies by Weihs (1973, 1981).

where $^{11}S_a = 1380$, and $^{12}S_b = 0.67$.

Caloric cost of activity¹³ was estimated as

$$ACT_{cal} = PWR * 20650,$$

where 20650 converts watts to calories/day. Power required to swim (PWR) was estimated as

$$PWR = MP / (ME * PE),$$

where MP is mechanical power required to overcome drag, ME is mechanical efficiency,¹⁴ and PE is "propeller efficiency" (efficiency of propulsion by flukes)¹⁵. MP (in watts) was estimated as a function of total drag (D_t ; in dynes) and velocity (VL; in cm/sec) as

$$MP = (D_t * L) / 10^7,$$

where the factor 10^7 converts the product $D_t * L$ to watts.

¹¹ S_a was assumed constant for all sizes of spotted dolphins. Given an observed rate of $0.45 \text{ mg O}_2 \cdot \text{g wet wt}^{-1} \cdot \text{hr}^{-1}$ for a spinner dolphin *Stenella longirostris* weighing 68000 WW_g (Hampton and Whittow 1976) and assuming 3.25 cal/mg O_2 (Elliot and Davidson 1975), then $2,386,800 (0.45 * 3.25 * 68000)$ calories are expended daily in standard metabolism, and $S_a = 1380 (2,386,800 / 68,000^{0.67})$. The observed resting rate of oxygen consumption is consistent with the range of resting rates ($0.3\text{--}0.6 \text{ mg O}_2 \cdot \text{g wet wt}^{-1}$) reported for bottlenose dolphins under various conditions (Hampton et al. 1971, Karandeeva et al. 1973, Hampton and Whittow 1976).

¹² Heusner (1982) presents convincing statistical arguments that intra-specific relationships between basal (standard) metabolism and body weight in adult mammals are better described by the $2/3$ power than the $3/4$ power proposed by Kleiber (1961). Heusner's argument is based on observed differences between adults of similar species (e.g., breeds of dog); but Huesner's curve is also more realistic because it predicts a relatively higher weight-specific rate in smaller (younger) animals of a given species. This is more consistent with Kleiber's (1961) observation that younger animals tend to have elevated weight-specific metabolic rates compared not only with adults of the same species, but with small adults of similar species. In young marine mammals, weight-specific standard metabolic rate is often at least twice the standard rate of adults (Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982). The parameterization above results in weight-specific estimates of S that are $2.3\text{--}1.3$ times higher in dolphins measuring $80\text{--}140 \text{ cm TL}$ than in adult dolphins ($\sim 190 \text{ cm TL}$). This differs by $0\text{--}11\%$ (increasing with increasing size) from basal metabolic rates of juvenile through adult seals of similar weight (Ashwell-Erickson and Elsner 1981).

¹³ Dolphins were assumed to swim steadily far enough below the surface to eliminate the effects of surface drag (e.g., Hertel 1969). This formulation ignores the costs of surfacing to breathe, and the attendant increase in total distance swum to follow a sinusoidal rather than a straight path through the water. Preliminary estimates of these additional costs for individual dolphins of several sizes, for reasonably realistic depths of dive and distance between surfacings, ranged from 10 to 25% of steady swimming costs. As this cost is relatively low, the dolphin model was not reformulated to include these added costs of surfacing.

¹⁴ $ME = 0.20$, by analogy to observed muscle efficiencies of terrestrial mammals.

¹⁵ $PE = 0.85$ by analogy to tunas (Magnuson 1978).

Total drag was estimated as a function of drag due to body, fins, and movements by flukes as

$$D_t = (0.5 * N * VL^2 * S_w * C_t) / (1.0 - FID),$$

where N is density of seawater (1.025 g/cm^3), S_w is wetted surface area of the body, C_t is coefficient of total drag, and FID is (fin + induced) drag. FID ¹⁶ is expressed here as the fractional increase in estimated total drag due to adding the effects of fins and moving flukes.

S_w is wetted surface area of the body, excluding flippers, dorsal fin, and flukes, estimated as¹⁷

$$S_w = 0.1636 * TL^{2.14}.$$

Surface areas of fins are excluded from this calculation because fin drag is incorporated into the equation for total drag as an increase of 21% over drag estimated from body dimensions alone.

C_t was estimated from the formula for drag of submerged streamlined bodies moving with constant velocity

$$C_t = C_f * [1 + (1.5 * (D_a / TL)^{3/2}) + (7 * (D_a / TL)^3)]$$

(Hoerner 1965, Webb 1975). C_f is the coefficient of friction drag, and D_a is the maximum body diameter (cm; derived from girth at axilla (G_a)) where

$$G_a = G_{aa} * WW_{kg}^{G_{ab}},$$

with $G_{aa} = 25$ and $G_{ab} = 0.28$, based on measurements of 50 spotted dolphins measuring $82\text{--}210 \text{ cm TL}$.

C_f was estimated from the equation for streamlined bodies moving submerged at constant velocity in turbulent flow as

$$C_f = 0.072 R_L^{-1/5},$$

where R_L is Reynolds number, estimated here as

$$R_L = (TL * VL) / v,$$

where v is kinematic viscosity ($= 0.01$ Stokes) assuming turbulent flow at the boundary layer (Webb 1975), and VL is velocity (cm/sec), estimated as

$$VL = VL_a * TL^{VL_b},$$

¹⁶ FID was assumed $= 0.21$, based on the fraction of estimated total (body + fin + induced) drag accounted for by (fin + induced) drag in the 4-dolphin sample.

¹⁷ Based on measurements of wetted surface area in the 34-dolphin sample.

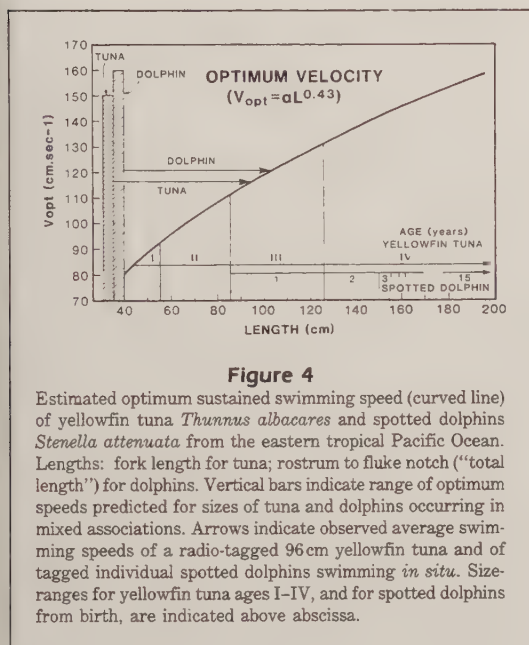


Figure 4

Estimated optimum sustained swimming speed (curved line) of yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* from the eastern tropical Pacific Ocean. Lengths: fork length for tuna; rostrum to fluke notch ("total length") for dolphins. Vertical bars indicate range of optimum speeds predicted for sizes of tuna and dolphins occurring in mixed associations. Arrows indicate observed average swimming speeds of a radio-tagged 96 cm yellowfin tuna and of tagged individual spotted dolphins swimming *in situ*. Size ranges for yellowfin tuna ages I-IV, and for spotted dolphins from birth, are indicated above abscissa.

where $VL_a = 20.6$ and $VL_b = 0.43$, assuming swimming velocity scales with length in the same manner for both spotted dolphins and yellowfin tuna (Fig. 4). Using the same formula and parameters to predict velocity as a function of length in both the tuna and dolphin models maintains comparability between results from the two models. As geometrically similar swimmers, hydrodynamic constraints should be approximately the same for both tuna and dolphins.

Specific rate of residual heat loss (HL_{rsp} ; calories heat lost in excess of that generated by active and standard metabolism, and specific dynamic action · calories of animal⁻¹ · day⁻¹)¹⁸ was estimated as

$$HL_{rsp} = HL_{usp} - (ACT_{sp} * (1.0 - ME) + STD_{sp} + SDA_{sp}),$$

where $HL_{rsp} > 0$, otherwise $HL_{rsp} = 0$.

¹⁸ Because spotted dolphins are warm-blooded relative to their environment and because their blubber layer is not a perfect insulator, they will constantly lose heat to surrounding water. If the sum of estimated heat production generated by muscle activity, standard metabolism, and specific heat of digestion equals or exceeds this unavoidable passive loss, the term has no effect. Otherwise, the additional heat loss was added to the animal's energy cost. In practice, the influence of the term was negligible, as differences between H_a and the sum of STD , ACT , and SDA were <10%.

The term $(1.0 - ME)$ in conjunction with ACT_{sp} expresses the fraction of total active metabolism that is dissipated as heat, rather than converted to mechanical energy. The term H_{rsp} was taken to be zero when the estimate of H_{rsp} yielded a negative result. In this case, all passive losses were more than offset by heat generated by metabolism.

Specific rate of unavoidable passive heat loss (HL_{usp} ; calories lost passively as heat · calories of animal⁻¹ · day⁻¹) was estimated following Brodie's (1975) procedure for passive losses in large whales,

$$HL_{usp} = \frac{((21.18/BD_a) * (37.0 - T_a) * S_m / 10000.0) * 24}{WW_g * (CD_d / 1000.0)},$$

where $^{19}BD_a$ is average blubber depth, CD_d is caloric density of spotted dolphins, 37.0 ($^{\circ}C$) is the assumed core temperature for spotted dolphins (Hampton and Whittow 1976), T_a is ambient temperature (assumed constant at $27^{\circ}C$), 21.18 is the conductivity factor for whale blubber (Brodie 1975), and $^{20}S_m$ is metabolic surface area, estimated as

$$S_m = 0.84 * S_w.$$

Unavoidable heat loss from fins and head is assumed negligible, as blood flow to these areas can be adjusted to minimize or maximize heat loss, as needed.

Specific dynamic action Specific rate of specific dynamic action (SDA_{sp} ; calories lost as heat of digestion · calories of animal⁻¹ · day⁻¹) was estimated as

$$SDA_{sp} = SDA * C_{sp},$$

where SDA (the fraction of consumption converted to heat energy during digestion) = 0.15 for both yellowfin tuna²¹ and spotted dolphins²².

Waste losses Specific rate of waste losses (WL_{sp} ; calories lost as feces or urine · calories of animal⁻¹ · day⁻¹) were estimated as the sum of fractional losses to egestion (F_a) and excretion (U_a)

¹⁹ $BD_a = 0.65$ cm, based on measurements of blubber depth at maximum girth for a sample of 72 spotted dolphins measuring 80–190 cm TL.

²⁰ S_m is the surface area of the body beneath the blubber layer. S_m averaged 84% of S_w in the 4-dolphin sample.

²¹ Reflecting the relative high-protein low-carbohydrate diet ingested by yellowfin tunas (Olson and Boggs 1986).

²² SDA is primarily a function of the protein content of ingested food, and is ~15% for a variety of carnivores, including sea otters eating clams and squid (10–13%, Costa and Kooyman 1984), harp seals eating fish (17%, Gallivan and Ronald 1981), and various terrestrial mammals fed a mixed diet (Kleiber 1961).

$$WL_{sp} = (F_a + U_a) \cdot C_{sp},$$

where $^{23}F_a = 0.20$ and $^{24}U_a = 0.07$ for yellowfin tuna; $F_a = 0.125$ and $U_a = 0.07$ for spotted dolphins²⁵.

Growth Specific rate of growth (calories available for growth · calories of animal⁻¹ · day⁻¹) was estimated as

$$G_{sp} = C_{sp} - (R_{sp} + SDA_{sp} + WL_{sp}).$$

Total calories available for growth (G_{cal}) is

$$G_{cal} = G_{sp} \cdot CAL_{an}.$$

Total grams wet-weight biomass available for growth (G_{wwg}) is then

$$G_{wwg} = G_{cal} / CD.$$

The formulas and parameter values presented above produce reasonable model estimates of the various energy fluxes for both yellowfin tuna and spotted dolphins (Edwards 1992).

Results: Estimated consumption

Despite the apparent similarity between yellowfin tuna and spotted dolphins in food **composition** (prey type and size²⁶), estimated food **requirements** for tuna and dolphins differ considerably. Estimated food requirements for individual tuna and dolphins imply that each dolphin requires 5–10 times more food per day than each yellowfin tuna, depending on the sizes of the tuna and dolphin being compared (Fig. 5). In a "typical" association of 200 dolphins and 500 tuna, total dolphin requirements are still 2–5 times higher than total tuna requirements per time-period (Fig. 6), despite the greater number of tuna than dolphins.

²³ Based on the relative assumed nondigestible portions of tuna diet items by analogy to similar items (Cummins and Wuycheck 1971).

²⁴ Based on measurement of non-fecal excretion by carnivorous fish (Brett and Groves 1979).

²⁵ Together these processes probably account for 15–20% of ingested food energy in spotted dolphins, as found for other small marine mammals eating fish (Shapunov 1973, Ronald et al. 1984, Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982, and references therein).

²⁶ Diet is undoubtedly an important factor in the tuna-dolphin association, as associated yellowfin tuna and spotted dolphins apparently have nearly identical feeding preferences (Perrin et al. 1973). Stomach contents of co-occurring tuna and spotted dolphins consisted primarily of small pelagic schooling fish (e.g., mackerel *Axaxis thazard*) and squid of similar types and sizes.

Discussion: Model implications

The strict "result" of exercising the models is estimation of food consumption by yellowfin tuna and spotted dolphins of various sizes. This information alone is not particularly helpful in furthering our understanding of the tuna-dolphin bond. However, the process of model

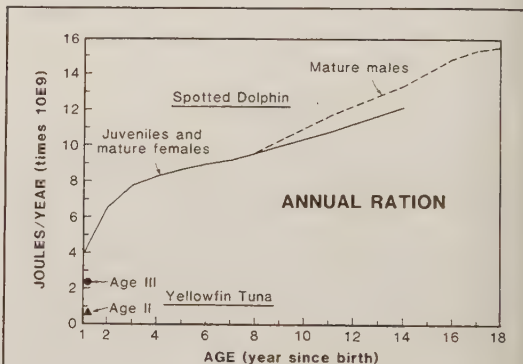


Figure 5

Estimated annual ration for individual spotted dolphins *Stenella attenuata* ages birth–18 yr, and yellowfin tuna *Thunnus albacares* ages II–III, occurring in mixed associations in the eastern tropical Pacific Ocean.

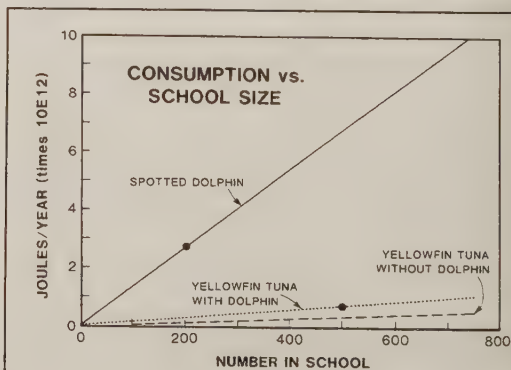


Figure 6

Estimated annual ration for schools of yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* occurring in mixed associations in the eastern tropical Pacific Ocean (ETP). Solid circles indicate number of individual dolphins and individual tuna in a typical mixed association. Ration estimates for schools were based on average observed size-frequency distributions of tuna and dolphin in the ETP.

development and comparisons of similar energy fluxes in the completed models generated several interesting observations with potentially significant implications.

Hydrodynamics and body length

Length frequencies of the tuna and dolphins in a typical association show a surprisingly strong overlap between age-III yellowfin and neonate-1st yr dolphins. Both animals begin their respective years at ~ 85 cm TL, and complete the year at ~ 125 cm TL (Fig. 4). This is significant for two reasons. First, this size range comprises the majority of the yellowfin tuna found associated with dolphins (Fig. 3)²⁷. Second, both animals have relatively stiff torpedo-shaped bodies with stiff fins and carangiform swimming behavior. Because theory predicts that optimum swimming speeds (the speed at which the least energy is consumed for a given distance covered) of geometrically-similar swimmers will be comparable (Weihs 1973, Webb 1975), the similar body forms and swimming behaviors of the tuna and the dolphins imply that optimum swimming speeds will also be similar for either animal of a given length.

Swimming speeds of sonic-tagged yellowfin tuna measured *in situ* show that individual undisturbed yellowfin, of the size most often found associated with dolphins, choose in their natural environment to swim on average at their predicted optimum cruising speed (e.g., yellowfin 90–100 cm FL swim at 100–130 cm/sec; Holland et al. 1990). Because yellowfin tuna tend to associate in schools of like-sized individuals, the expected speed of the tuna group is similar to the expected speed of the individuals involved.

In contrast, tracking studies (Perrin et al. 1979) of spotted dolphins in the ETP indicate that dolphin schools swim on average not the speed most efficient for the majority of the individuals in the school (i.e., ~ 160 – 170 cm/sec for large adults) but the speed most efficient for the neonate-1st yr animals (~ 120 cm/sec; Fig. 4).

These observations imply that yellowfin associating with dolphin schools may do so at little or no added hydrodynamic cost. The associated fish, unlike larger or smaller sizes of yellowfin, need swim neither faster nor slower than their apparently preferred optimum in order to maintain an association with dolphins.

The observation that associating with dolphins may cost tuna little does not explain why the tuna par-

ticipate. The similarity in feeding preferences and probable similarity in feeding behaviors provides one explanation and suggests that tuna are more likely to follow dolphins than the reverse.

Who follows whom

The higher forage requirements of dolphins both individually and as an association imply that dolphins following tuna, particularly single dolphin schools following single tuna schools, would fall far short of meeting their daily energy requirements. Dolphin schools might avoid this energy deficit by switching from one tuna school to another, but they would have to switch consistently from recently-successful to soon-to-be-successful schools of foraging tuna. This frequent switching could be difficult because it would likely involve periods of searching at speeds greater than sustainable by the young dolphins, in order to find new tuna schools (and new patches of forage) faster than the patches could be found by the current tuna school.

Measurements of muscle mass and estimates of power-time curves for various sizes of spotted dolphins imply that the relatively small muscle mass of neonate-1st yr dolphins probably cannot sustain speeds much faster than their predicted optimum for any extended length of time (unpubl. data). If searching for new schools of tuna requires sustained accelerated swimming, the young dolphins could have trouble keeping up with the rest of the school. Because it is unlikely that dolphins, as nursing mammals and highly social animals, would simply leave their young behind, switching frequently from one tuna school to another may not be a practical option.

The disparity in feeding requirements implies that, while dolphins would probably be disadvantaged by having to rely upon tuna to locate sufficient prey, the tuna could recognize an advantage by following dolphins. The fish would then be associating with another predator that is searching for the same prey, but which must encounter that prey either more often or in considerably larger patches than required by the tuna, per time period.

However, the greater need of the dolphins for food implies concomitantly that competition for resources, if those resources are limited, could be fierce. The schooling characteristics of the predators and prey, coupled with feeding behaviors and differing sizes of the predators, provide one possible explanation for the ability of the smaller yellowfin tuna under some circumstances to persist in this potentially competitive association despite the dolphin's greater size, and need for food.

²⁷ Figure 3 includes fish from all areas of the fishery, not just the offshore areas where most dolphin fishing occurred during the years these data were collected, causing dolphin-fish distribution to be skewed to left.

WHEN SHOULD TUNA ASSOCIATE WITH DOLPHIN?

PREY ABUNDANCE: PATCH TYPE:	LOW		HIGH	
	RARE LARGE	FREQUENT SMALL	RARE LARGE	FREQUENT SMALL
ABILITY TO LOCATE PREY:				
D > T	YES	NO	YES	NO
D = T	NO	NO	NO	NO
D < T	NO	NO	NO	NO

Figure 7

Decision table predicting conditions under which yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* should (or should not) associate.

Avoiding competition for food

As is characteristic of pelagic ocean systems, both predators and prey in the ETP occur in clumped distributions. Individuals occur in schools or aggregations separated by (often vast) distances devoid of other individuals. The prey, like the yellowfin tuna, will tend to occur in schools of like-sized individuals with similar swimming speeds. Aggregations of tuna and dolphins will typically consist of dolphins of assorted sizes accompanied by tuna of approximately one size. The feeding strategy of the predators will involve searching for a clump of prey, simultaneous (or nearly so) arrival at the prey patch by both tuna and dolphins, and repeated incursions by individuals of both predator groups into the clump of prey wherein prey are seized and swallowed whole individually.

Associated yellowfin tuna may be able to mitigate this direct competition with dolphins for food on the basis of the difference in size between the fish and the feeding adult dolphins (~100 cm vs. 200 cm TL). Because the tuna are smaller, they have smaller maximum stomach capacity (~400 g wet wt for age-2 yellowfin, ~1100 g wet wt for age-3 yellowfin; Olson and Boggs 1986) compared with spotted dolphins (~2000 g wet wt in adults; Bernard and Hohn 1989). Even if the smaller, presumably more-agile tuna could seize individual prey only as fast as the dolphins and no faster, they would satiate more quickly than the dolphins.

As both groups would begin feeding at the same time, when the prey concentration was maximum, the tuna at any time would be relatively closer than the dolphins to satiation, given the observed (average) relative proportions of tunas and dolphins in a typical association.

The tuna would be filling their stomachs while the prey were still relatively dense. Depending on the size of the prey patch, dolphins might never succeed in satiating, even though the tuna had their fill. Even if the prey patch was sufficiently limited that neither group achieved satiation, the tuna would always be relatively more full at any given time. Thus, although the dolphins require more prey overall, the tuna could succeed competitively by satiating sooner (being relatively more successful) during any given prey encounter.

However, it may not always be to the tuna's advantage to associate with dolphins, even given this scenario. The benefit (or not) can be assessed by evaluating the relative advantages of associating or not, given the range of possibilities for prey spatial distribution and abundance.

When should the association occur?

The possibilities can be summarized in a simple decision table (Figure 7). At the extremes, prey abundance may be either low or high and any given abundance may be either homogeneously distributed (frequent) or clumped (rare). The possibilities for locating prey are that (1) dolphins are more adept than tuna, (2) both are equally adept, or (3) dolphins are less adept than tuna. The advantages for tuna to associate with dolphins can be assessed for each cell in the table.

Consideration of each cell in the table suggests that tuna may benefit from associating with dolphins only when (1) prey are distributed in rare patches and (2) dolphins are more adept than the tuna in finding these patches. This would be true regardless of prey concentration within the patches, because whenever tuna and dolphin associate they will compete for food. If tuna are more adept than dolphins at finding food, then there will be no foraging-related advantage for the tuna to associate with their competitors. The tuna would be able to find food more easily on their own than by following dolphins, and would not have to risk sharing these resources once located. If the tuna and dolphins are equally adept, there is still no advantage, for the same reason.

If the prey are distributed in relatively small but numerous patches, there is still no advantage for tuna to associate with dolphins, again because the spatial frequency of schools would produce a relatively high probability of tuna encountering the food on their own without risk of sharing with their competitor. In addition, when patches are small, the tuna would be especially disadvantaged by having to compete with dolphins because the presence of dolphins could prevent the tuna from satiating, despite the fact that the tuna would still be relatively more full than the dolphins when the patch had been exhausted.

But when the prey are distributed in rare patches and the dolphins are more adept than the tuna at locating these patches, then tuna could benefit from associating with dolphins because the fish could encounter food more often than if they were not associated. This will be true regardless of the density of the prey patch.

It is never the case that dolphins benefit energetically from depending entirely on tuna for finding prey, because dolphin forage requirements are so much higher than tuna requirements.

These conclusions lead to the hypothesis that tuna-dolphin associations should be more prevalent in areas where oceanic conditions encourage strong clumping of prey, and less prevalent when conditions encourage a more homogeneous distribution of prey. I am currently exploring, with a simulation model of tuna, the movements of dolphin and prey in response to environmental characteristics of the ETP (work in progress). Further studies correlating oceanic environmental characteristics with catches of various size-classes of tuna are planned but not yet underway. If the suggestions described above are borne out, it may be possible to identify areas of the ETP where large yellowfin tuna could be captured without having to rely on dolphin-associated fishing.

Caveats

This study assumes that average size of dolphin schools remains constant at about 200 animals. This is the average school size for spotted dolphins observed during dolphin survey research cruises in the ETP. In fact, neither school size nor school composition are constant. Observers on both research and commercial vessels report school sizes ranging from a few animals to many hundreds. Scott (1991) reports diel changes in sizes of schools sighted by tuna fishermen in the ETP.

However, these inconsistencies may not significantly affect the implications of the energetics estimates presented here. Average sizes of dolphin schools captured with tuna in the ETP are considerably larger (400–600 animals) than the average school size observed during research surveys because the fishermen preferentially search and capture large schools of dolphins, which tend to carry more tuna. Estimates concerning the relative importance of tuna and dolphins to energetics of the association are probably reasonably similar for both large and small associations, because in both cases the proportions of tuna and dolphins tend to be similar (i.e., as the number of dolphins increases, in general the number of associated tuna increases). The study of diel differences (Scott 1991) shows that school sizes of dolphins sighted in association with tuna vary from a morning low to a late-afternoon high, but

the change is relatively small, from ~450 to ~600 animals on average.

Other explanations for the bond

Other hypotheses have been proposed to explain the tuna-dolphin association. The two most-often suggested are the possibility that tuna perceive dolphin schools as FADs (fish aggregating devices) or as protection from sharks. Both of these factors may well contribute to the strength of the bond; neither precludes the energetics results discussed above.

The propensity for fish to collect around floating objects is well known, although the reasons are not yet understood. Presumably, floating objects provide a reference point for the aggregating tuna and in some way increase foraging success, perhaps by concentrating prey items or by tracking convergence areas where prey densities may be higher than elsewhere.

The FAD hypothesis has merit for the sizes of tuna actually found with dolphins in the ETP, for two reasons in particular. First, associating with dolphins may increase foraging success for the associated tuna because both tuna and dolphins are apparently seeking the same prey and dolphins may be more adept at finding it. Thus, tuna are associating with a FAD that does not simply attract appropriate prey passively, but actively searches and finds it. Second, tuna are required to swim constantly in order to ventilate their gills. It appears convenient that the average observed speed of dolphin schools is also the optimum speed of the sizes of tuna usually found associated with these schools. Rather than circling a stationary FAD, tuna associated with dolphin schools will cover a much larger area while moving at their most efficient cruising speed, and will cover that area in the presence of a sentient foraging FAD.

The shark protection hypothesis derives from a common perception that dolphins actively protect their young by driving sharks from their vicinity. If this is so, tuna associating with dolphins may be associating with the best of all possible FADs; a floating object that moves at the tuna's optimal speed, moves in search of the same prey the tuna would like to find, is probably at least as adept as the tuna at finding that preferred prey, and which provides protection against, rather than increased risk of, predation (FADs of course concentrate not only fish, but also their predators).

Both the FAD and shark hypotheses assume that tuna follow dolphins. Not all hypotheses assume that tuna are the followers. Au and Pitman (1986) and Au (1991) suggest, for example, that dolphins follow tuna in order to take advantage of tuna foraging in conjunction with bird flocks. This would be an advantage for dolphins during the actual feeding event. However, it

does not solve the problem that dolphins apparently must locate not only the same type of prey as large yellowfin tuna, but quite a bit more of it during any given time-period. Following tuna does not appear adequate to fulfill dolphin schools' energy requirements.

This fundamental difference in food energy requirements may be the single most important biological factor underlying the association. Oceanographic conditions (the shallow mixed layer)* set the stage; energetics requirements (hydrodynamics and foraging patterns) appear to constrain the roles. Although the definitive answer has yet to be demonstrated quantitatively, the energetics-based hypotheses presented here are at least consistent with currently available data. The tuna-dolphin association may be a consequence of a combination of oceanography, hydrodynamics, foraging energetics, and life-history characteristics, i.e., a consequence of the ecology of the association's components.

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Power to detect linear trends in dolphin abundance: Estimates from tuna-vessel observer data, 1975-89

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Trends in abundance of dolphin stocks affected by the tuna purse-seine fishery in the eastern tropical Pacific Ocean (ETP) are of intense interest to a number of organizations concerned about the stocks' continued survival (Hammond and Laake 1983, Gerrodette 1987, Holt et al. 1987, Buckland and Anganuzzi 1988, Anganuzzi and Buckland 1989, Anganuzzi et al. 1991). The most straightforward method for estimating such trends is linear-regression analysis of relative abundance indices across time (e.g., Anganuzzi and Buckland 1989). Such abundance indices can be derived from data collected by observers aboard the tuna vessels (Buckland and Anganuzzi 1988, Anganuzzi and Buckland 1989, Anganuzzi et al. 1991). Linear trends in abundance over successive 5-year periods have been reported by Buckland and Anganuzzi (1988), Anganuzzi and Buckland (1989), and Anganuzzi et al. (1991).

Power analysis provides a method to quantify the probability of not detecting low rates of change in abundance over a specified time-period. It also provides a method, in cases where no statistically-significant trends are apparent, for determining the steepness of change necessary for its statistical detection given observed variability in the data, i.e., detectable trend (Gerrodette 1987, Peterman 1990). We use power analysis here to assess the efficacy of weighted linear-regression analysis for estimating

linear trends in abundance of eight stocks of ETP dolphins. While it is instructive to evaluate the power of conclusions about observed trends, it is perhaps even more important to determine the magnitude of change required for detection of a trend, given observed variability in the dolphin abundance estimates. Therefore, we also calculate detectable trends, in addition to power of observed trends.

We present here estimates of observed trend, power to detect trends, and detectable trends for eight stocks of ETP dolphins, over time-series of 5, 8, and 10-years, assuming a two-sided hypothesis with $\alpha = 0.10$, using the noncentral *t*-distribution for the alternative hypothesis. Detectable trends were estimated assuming Type I (α) and Type II (β) error levels equal 0.10. We estimated power and detectable trends for all three sets of time-series to determine how much improvement might be expected by increasing the number of years included in the trend estimate. We did not include longer time-series, as it is unlikely that even a population with reproductive and individual growth rates as relatively slow as ETP dolphins would follow a linear trend for more than a decade, if that long.

Methods

Relative abundance indices and their associated bootstrap standard errors for eight stocks of ETP

dolphins during the years 1975-89 (Table 1, Fig. 1) formed the database for the regression analyses presented here. Indices and standard errors for 1975-87 were taken from Anganuzzi and Buckland (1989), and for 1988 and 1989, from Anganuzzi et al. (1991). The eight dolphin stocks included northern offshore and southern offshore stocks of the pantropical spotted dolphin *Stenella attenuata*, the eastern spinner dolphin *Stenella longirostris orientalis*, northern and southern stocks of whitebelly spinner dolphin (hybrid/intergrades between *Stenella l. orientalis* and *Stenella l. longirostris* [Perrin 1990]), and northern, central and southern stocks of the common dolphin *Delphinus delphis*.

Observed trends

We estimated linear trends in relative abundance for each of the eight stocks over sequential series of 5, 8, and 10 years, using standard weighted least-squares regression (Wilkinson 1989). The slope of the regression (*b*) estimates the trend in abundance. The estimated standard error of the estimated trend (*s_b*) indicates the variability associated with the trend estimate. Weights were the reciprocal of the square of the bootstrap standard errors (Buckland and Anganuzzi 1988). We eliminated the estimate for 1983 from all analyses, because the presence of a very strong El Niño that year caused biologically unreasonable estimates of abundance for many of the stocks, in particular for northern offshore spotted dolphins, the stock affected by the fishery in greatest numbers (Buckland and Anganuzzi 1988, Anganuzzi et al. 1991). In the absence of any objective criteria for choosing which stocks were (or were not) affected by the El Niño, we elected to treat

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Table 1

Estimated abundances (first row) and bootstrapped standard errors (second row) for eight stocks of dolphins affected by the tuna purse-seine fishery in the eastern tropical Pacific Ocean. Values are in thousands. Data for 1975-87 from Buckland and Anganuzzi 1988; data for 1988-89 from Anganuzzi and Buckland 1989. Dashes indicate no values reported for that year. Asterisks indicate values from 1983 omitted as anomalous. SOPS boundaries (Anganuzzi and Buckland 1989) used in estimating southern offshore spotted dolphins. See text for scientific names.

	Dolphin stocks							
	1	2	3	4	5	6	7	8
1975	3949	—	599	490	—	122	404	385
	996	—	197	181	—	51	138	227
1976	4253	574	535	1205	115	344	287	586
	908	212	190	293	62	130	80	223
1977	3828	924	514	588	203	637	466	229
	751	332	152	163	87	200	90	162
1978	3212	584	395	613	65	358	329	—
	543	302	124	150	47	126	105	—
1979	2950	1040	428	366	—	650	644	—
	559	394	202	183	—	248	287	—
1980	3335	260	447	342	124	512	251	230
	582	168	112	99	86	191	85	139
1981	2536	199	255	694	124	513	111	435
	443	83	165	287	80	330	35	142
1982	2550	591	202	416	100	—	232	103
	557	180	91	132	47	—	101	90
1983	*	*	*	*	*	*	*	*
	*	*	*	*	*	*	*	*
1984	2158	244	340	253	182	—	71	—
	362	115	85	72	71	—	91	—
1985	2884	238	586	648	247	—	265	249
	352	68	124	128	64	—	105	318
1986	3165	154	584	451	—	475	169	—
	302	60	108	95	—	237	50	—
1987	2953	—	384	650	—	304	60	—
	293	—	87	105	—	123	18	—
1988	2689	79	717	484	88	323	241	253
	326	30	110	92	33	93	50	100
1989	2910	560	389	515	190	243	125	179
	275	140	71	78	69	107	24	47

- 1 = northern offshore spotted dolphin
 2 = southern offshore spotted dolphin
 3 = eastern spinner dolphin
 4 = northern whitebelly spinner dolphin
 5 = southern whitebelly spinner dolphin
 6 = northern common dolphin
 7 = central common dolphin
 8 = southern common dolphin

all eight stocks similarly by eliminating the 1983 estimate.

For each series, we calculated regressions using as many data points as existed for each species for that

number of years. In some cases, this resulted in as few as three data points contributing to the regression. Because we omitted data from 1983, the 10-year series contained at most nine data points. Because some years were omitted or were missing abundance indices, not all year-series comprised strictly consecutive x-values (year values).

We reexpressed the slope estimate of trend (b) in terms of a change parameter r , where

$$r = b/A_1$$

and A_1 (estimated abundance in first year of series) is calculated from the estimated slope and intercept for each year-series. For these linear regressions, the parameter r expresses the annual rate of change as a fraction of the estimated initial abundance (Gerrodette 1987). Linear regressions were calculated only for series with at least three data points.

Power

We estimated power of statistical conclusions about the significance of each slope by assuming a two-sided alternative hypothesis and using the non-central t (nct) distribution. In all cases, we assumed error levels $\alpha = \beta = 0.10$. We used a two-sided hypothesis test to be consistent with earlier estimates of 5-year trends in abundance (Buckland and Anganuzzi 1988, Anganuzzi and Buckland 1989, Anganuzzi et al. 1991).

To calculate power using the nct distribution, we utilized a series of programs (available upon request) designed to return power estimates as a function of three input variables:

$t_{\alpha,df}$ = normal t statistic given a level of α and degrees of freedom,

IDF = degrees of freedom, and

$\delta = b/s_b$.

Degrees of freedom were $n - 2$ where n is the number of years for which abundance estimates existed in a series. Values for b and s_b were calculated from the weighted linear regressions.

δ is the offset of the alternative distribution (the nct) standardized by the standard error of the offset. In all cases, we assumed as the alternative distribution the observed trend for a series. δ is thus the distance, expressed as standard deviation units, between the mean of the null distribution (taken here to be zero slope) and the mean of the alternative distribution (the slope estimated from regression of the data).

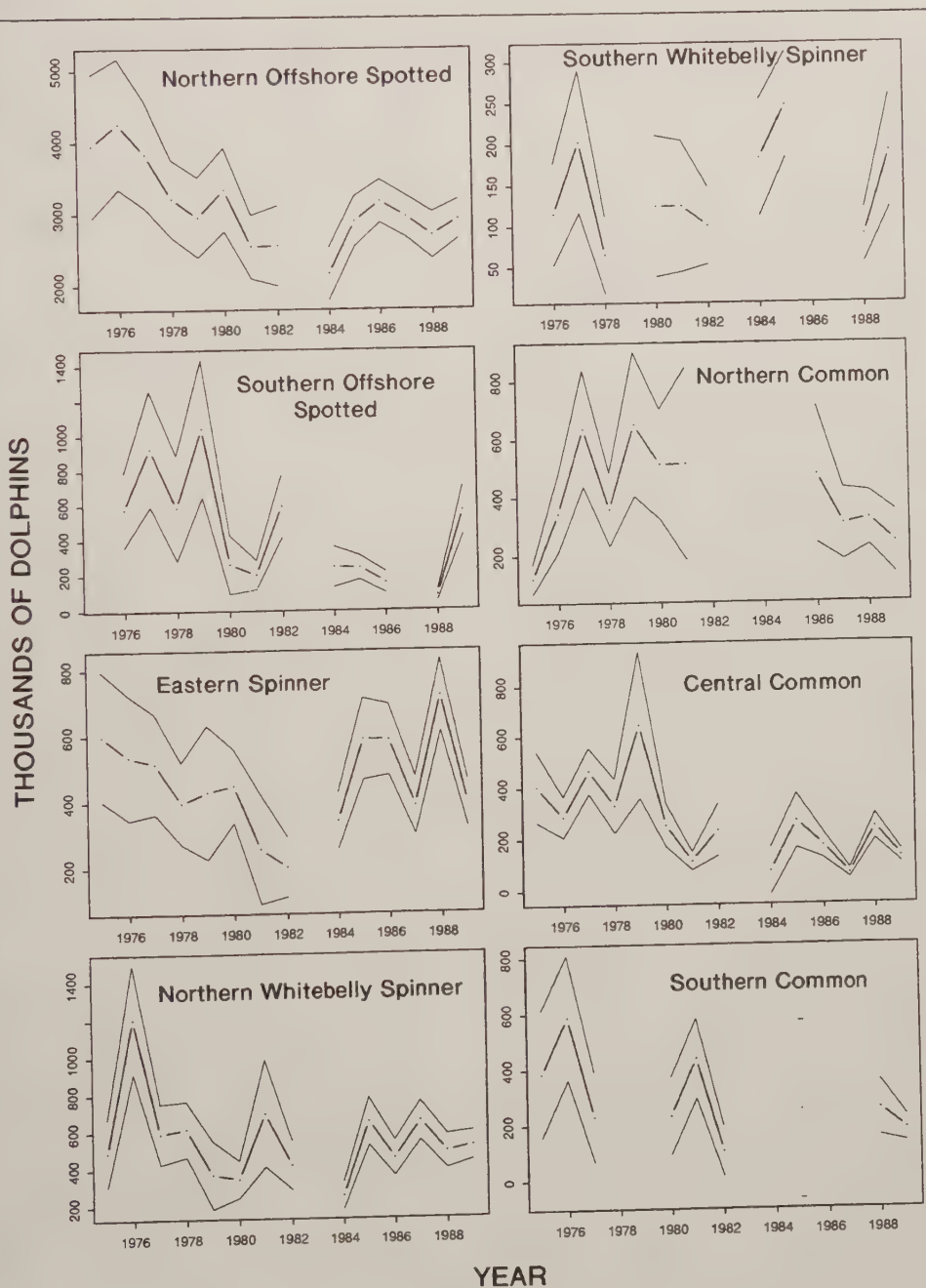


Figure 1

Estimated abundances (dashed line) of dolphins bounded by 1 bootstrap standard error (solid lines). Years for which no estimates were reported are omitted; estimates for 1983 are omitted as anomalous.

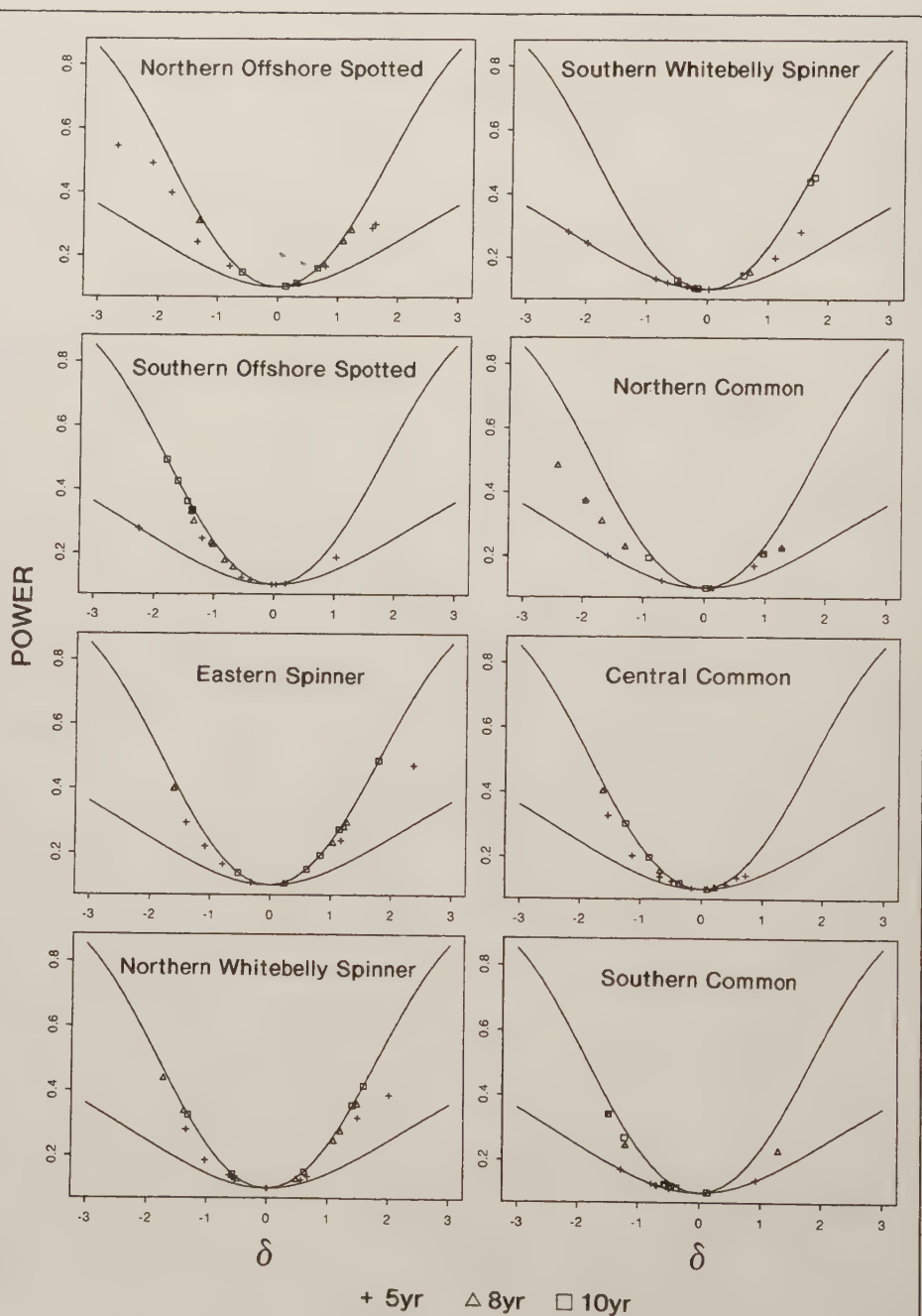


Figure 2

Power of conclusions about lack of statistical significance for estimated 5, 8, and 10-year trends in dolphin abundance. Power calculated for two-tailed noncentral t , assuming $\alpha = 0.10$. Solid lines indicate maximum (7 df) and minimum (1 df) power envelope. δ is the noncentral t parameter.

Detectable trends

We estimated detectable trends (r_d) for all data-series. All estimates of r_d assume error levels $\alpha = \beta = 0.10$. Detectable trends were estimated by determining the value of Delta ($\delta_{0.9}$) that returns a power value of 0.90 from the net algorithm. As before, input value for IDF was $n - 2$, and for s_b was the value estimated from the weighted regression. Then the value of b generating the desired power level (b_{net}) is

$$b_{\text{net}} = \delta_{0.9}/s_b$$

and the detectable initial trend per year is

$$r_d = b_{\text{net}}/A_1.$$

Results

Observed trends

The majority (151/192; 79%) of the series showed no significant trend (specific data available from the authors). Of those that did, most showed decreases prior to the mid-1980s and no consistent trends since. Where population-abundance indices changed relatively regularly over time, successively longer time-series retained the same general patterns as found in shorter series. For example, observed trends were significantly negative for northern offshore spotted dolphin during the 5-year series 75/79 and 77/81, the 8-year series 75/83, 76/83, and 77/84, and the 10-year series 75/84 and 76/85. Similarly, 5-year negative trends were also reflected in 8- and 10-year series for southern offshore spotted dolphin, eastern spinner dolphin, northern whitebelly spinner dolphin, and central common dolphin.

Data were so sparse and variable for southern whitebelly spinner dolphin and southern common dolphin that little can be said about trends in these stocks. Northern common dolphin were the only species for which trends may have switched during the period of investigation (from negative during earlier years, to positive more recently); but it is obvious that here, as in the other series, the pattern in trend estimates is simply a function of the length of the series selected and its placement in time.

Power

Power to reject a false null hypothesis increases with increases in either or both of series length (as degrees of freedom increase) or δ (offset) (Fig. 2), but for TVOD the increases generally were not sufficient to be of

practical use. Where no significant trends (slopes) were found, power to detect a false null hypothesis was low, averaging 20–30% in most cases and never exceeding 60%. Power for each test was small because the alternative hypothesis for these power calculations was taken to be the observed slope, which was usually fairly small, and also because scatter around the regression line tended to be large. Therefore the null and alternative distributions overlapped considerably. The low power of these tests simply means that if the true slope equaled the observed slope, the power to distinguish the true slope from a slope of zero (i.e., no change in abundance) would be quite small in most cases.

Detectable trends

The range of detectable trends decreased rapidly with increasing series-length in all cases (Fig. 3), as this increases the degrees of freedom (number of data points). The decrease is misleading in most cases, however. Although the improvement in ability to detect smaller trends with longer time-series appears dramatic, in most cases even the smallest detectable trends are still much too large to be of use.

Even with as many as 10 years of data in a series, linear trends less than about 10% per year could be detected consistently only for northern offshore spotted dolphin. For all other stocks, trends of at least 15–20% per year would be required to produce a significant result (Fig. 2). Series lengths would have to be such that populations more than doubled or decreased to zero in order for the change to be statistically detectable. This would require series lengths of at least 10 years.

In many cases, where significant trends were found, these trends were of lesser magnitude than the estimated detectable trend. This occurs because the estimated detectable trend is the expected value of the alternative distribution. Any trend value which falls below this expected value, but which also falls above the Type-I error limit for the null distribution, will be assumed significantly different from the null even though the trend could actually belong to either distribution. For example, if the Type-I error limit for the null distribution occurs at a trend value of 0.75 (i.e., if the cut-off point for values assumed to belong to the null distribution is 0.75), and the expected value (i.e., the mean) for the alternative distribution falls at 0.85, any trend value within the range 0.75–0.85 will be assigned to the alternative distribution even though it is smaller than the expected value of the alternative distribution. In practice for the ETP data, this effect is unimportant compared with the overall problem of high variability obscuring the possibility of detecting managerially-relevant trends in abundance (i.e., the

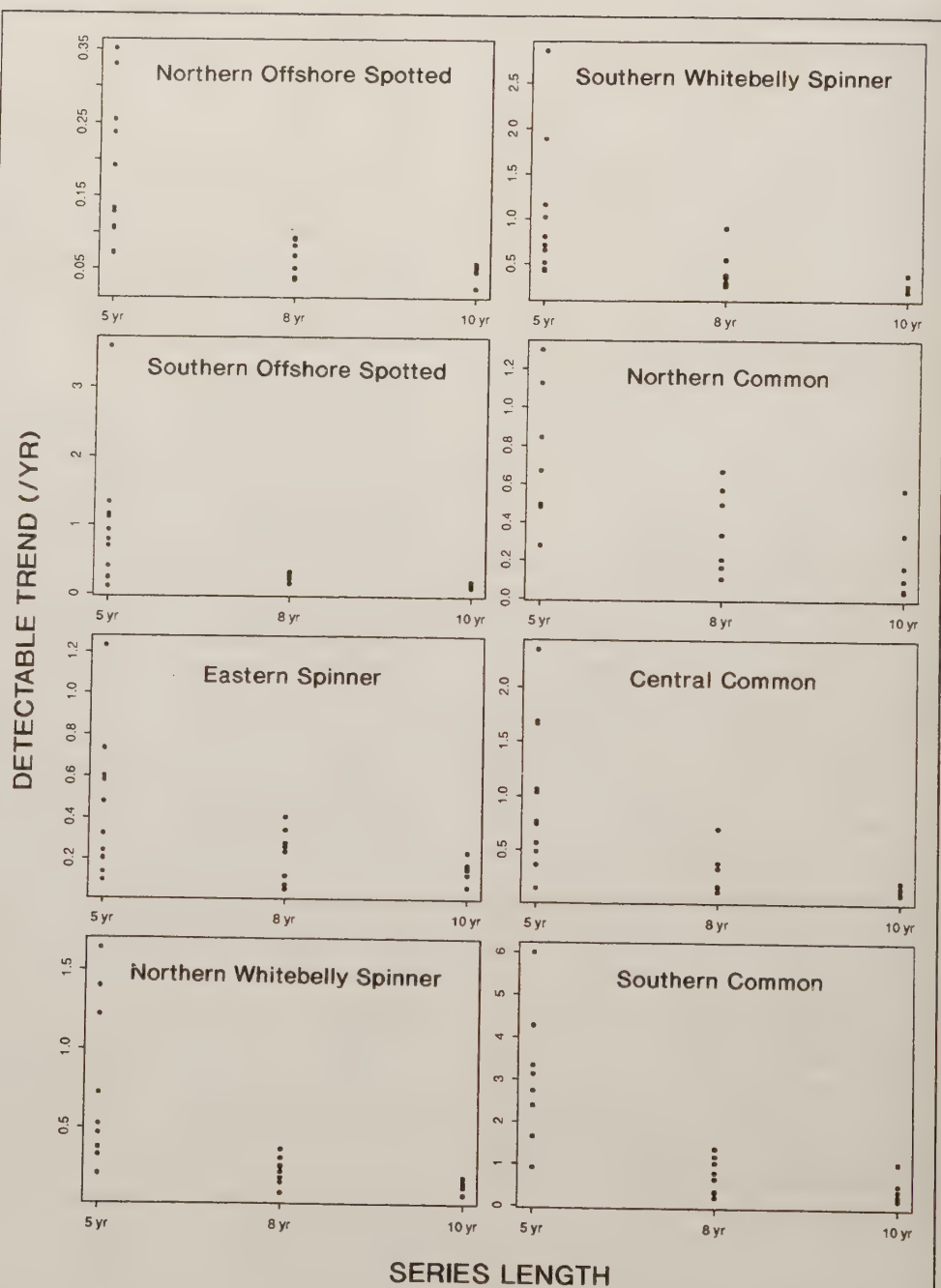


Figure 3

Estimated detectable trends for successive 5, 8, and 10-year series of tuna vessel observer data.

spread and subsequent overlap between null and alternative distributions is so great that differences between the cut-off point in the null and the mean of the alternative is effectively inconsequential).

Discussion

Given the observed variability in TVOD, it does not appear that linear trends in dolphin abundance estimated from these data with these techniques will be detectable at any levels practical for management purposes, except possibly for the stock of northern spotted dolphin. Even for this stock, survey series at least a decade in length are required.

Our estimates of 5-year trends agree with previously published estimates derived by the same methods, where 1983 has been omitted from the analyses (Anganuzzi and Buckland 1989). Our results imply that for time-periods as short as 5 years, considerably larger trends than those observed would be necessary to produce estimates of significant change with any reasonable power. Except for northern offshore spotted dolphin, this applies also to all other stocks, even for the maximum time-series tested (10 years in this study). It appears that other methods must be found to determine whether trends truly exist in dolphin abundance in the ETP. For management purposes, longer time-series must be monitored, for which linearity cannot be assumed. Other regression procedures making greater use of the precision estimates (standard errors) of the indices could have more power, but for linear analyses, at least, it is uncertain whether the increase in power could overcome the inherent variability and probable nonlinearities in the data.

A more effective approach to estimating trends in dolphin abundance is probably represented by the sophisticated smoothing method applied recently to these data by Buckland et al. (1992). The method reduces the relatively-scattered abundance estimates to smoothly-changing estimates of abundance, but with the advantage of producing confidence limits about the smoothed trend and generating a more biologically-reasonable result (abundance of natural populations rarely changes linearly). However, simulation experiments will be required to determine the circumstances under which the smoothed trends do, or do not, reflect accurately the true underlying dynamics of the stocks. Such simulations are currently underway, but results are as yet unavailable (Alejandro Anganuzzi, Inter-Am. Trop. Tuna Comm., La Jolla, pers. commun., July 1991).

Regardless of the results of the tests of various smoothing methods, it appears fruitless, based on the results presented here, to use linear-regression tech-

niques to estimate trends in abundance of dolphin stocks in the ETP, even for periods as long as a decade. The power to detect ecologically (or managerially) relevant trends, given the observed variability in the data, is simply not sufficient.

Future efforts should, as suggested by Buckland et al. (1992), focus on developing or applying robust, curvilinear smoothing techniques that are reasonably responsive to the underlying processes or mechanisms controlling actual changes in dolphin abundance.

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Evaluation of Rectangular and Circular Escape Vents in the Northwestern Hawaiian Islands Lobster Fishery

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Abstract.—Research was conducted in Hawaii during 1984–1987 to investigate the possibility that escape vents fitted in traps used by the commercial lobster fishery in the northwestern Hawaiian Islands would reduce the catch and mortality of sublegal spiny lobsters *Panulirus marginatus* (<50 mm tail width) and slipper lobsters *Scyllarides* spp. (<56 mm tail width) without significantly reducing legal catch. A circular vent was more efficient than the traditional rectangular vent in maximizing escapement of sublegal lobsters and retention of legal ones for both species. Optimum results were attained with two vented panels each containing four 67-mm-diameter circular vents. Traps equipped with the circular vents caught 83% fewer sublegal spiny lobsters and 93% fewer sublegal slipper lobsters than nonvented control traps, and they did not significantly reduce legal catch of either species. In contrast, traps with two 49-mm-high × 285-mm-wide rectangular vents reduced the catch of sublegal spiny and slipper lobsters by 70 and 93%, respectively, but also reduced legal slipper lobster retention by a significant 32% of the control catch. As a result of this research, all traps used in the lobster fishery in the northwestern Hawaiian Islands after 1 January 1988 must be equipped with two panels with 67-mm circular vents. The 1988 catch of sublegal spiny lobsters declined by 38% at Necker Island, northwestern Hawaiian Islands, whereas the legal catch increased substantially.

The mortality of sublegal lobsters (i.e., below minimum legal size) after they are trapped and released is a major problem in lobster fisheries throughout the world. Factors contributing to this mortality include direct physical damage caused by handling, displacement from home reefs, and increased predation resulting from weakened condition after release (Brown and Caputi 1986; Hunt and Lyons 1986; Lyons 1986). The problem is important because even low mortality can result in the loss of substantial revenue to a fishery when the loss of potential reproduction is added to the value of individual lobsters. Escape vents fitted onto the sides of traps have been used to reduce sublegal mortality in lobster fisheries in Canada (Wilder 1949), California (Lindberg 1955), Australia (Bowen 1963), New Zealand (Ritchie 1966), and New England (Krouse and Thomas 1975) and have been proposed for use in Florida (Lyons and Hunt, in press).

The present commercial lobster fishery in Hawaii is largely confined to a string of atolls and banks northwest of the island of Niihau and collectively referred to as the northwestern Hawaiian Islands (Figure 1). This fishery expanded rapidly after 1976, when a single vessel began trapping spiny lobsters *Panulirus marginatus* at Necker Island (Uchida and Tagami 1984). The fishery exploits *P. marginatus* and several species of slipper lobsters *Scyllarides* spp. *Scyllarides squammosus*

constitutes up to 90% of the slipper lobster catch (R. P. Clarke, P. A. Milone, and H. E. Witham, Southwest Fisheries Science Center, unpublished data). Hereafter, spiny and slipper lobsters will refer to *P. marginatus* and *S. squammosus*, respectively. Current regulations prohibit the harvest of spiny lobsters of less than 50 mm tail width (TW) and slipper lobster of less than 56 mm TW (Western Pacific Regional Fishery Management Council, 1985 and 1987, Honolulu, Hawaii). In 1986 nearly 900,000 legal spiny lobsters (521 tonnes) and about 1.4 million slipper lobsters (484 tonnes) with a combined ex-vessel value of US\$6.0 million, were landed in the northwestern Hawaiian Islands (Clarke, Milone, and Witham, unpublished data), making this one of the most lucrative commercial fisheries in Hawaii. Total spiny lobster catch in 1986 was 1.4 million animals, 22.6% of which were sublegal and had to be released. No minimum-size limit was in effect for slipper lobsters prior to March 1987, but a substantial portion of the catch consisted of individuals below the current legal size.

The effect of vented traps on the escapement of sublegal spiny lobsters was initially addressed in Hawaii from 1979 to 1982 (Paul 1984). Early results proved promising, so research on escapement of sublegal spiny lobsters was continued during 1984 (Skillman et al. 1984). The ultimate goal of the present study was to develop an escape vent

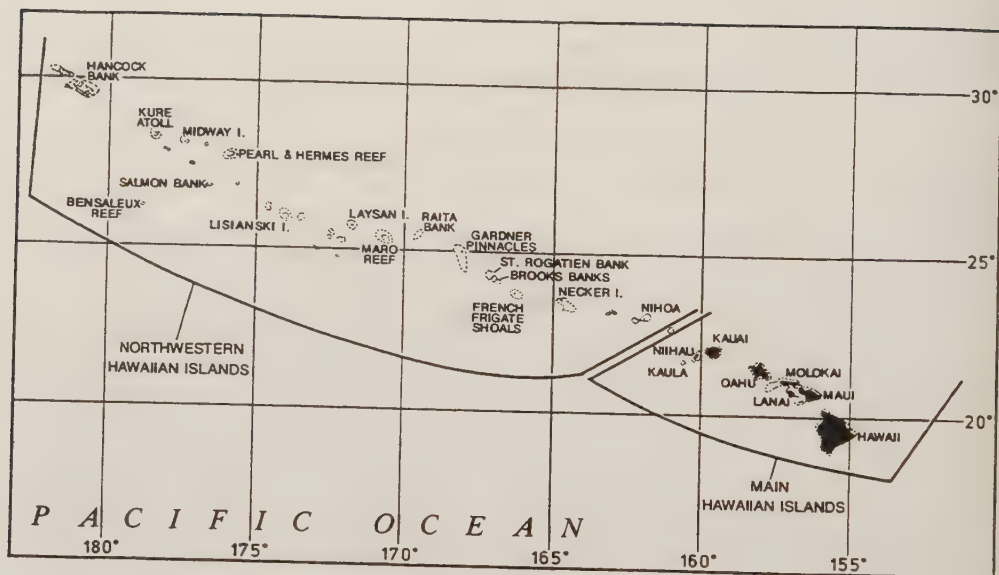


FIGURE 1.—The Hawaiian Archipelago.

that would allow sublegal lobsters of both major species to escape without significantly compromising legal catch.

Methods

The experimental design, originally proposed in March 1984 (Skillman et al. 1984), consisted of four research phases designed to determine the optimum escape vent size for spiny lobsters. In phase 1, the vent size was estimated by simply passing legal spiny lobsters through various-sized rectangular openings. In phase 2, this preliminary estimate was used to set up and conduct laboratory escapement trials based on a response surface model (Cochran and Cox 1957). During phase 3, these laboratory estimates of escape vent size were refined by conducting field trials aboard the National Oceanic and Atmospheric Administration ship *Townsend Cromwell* on the same fishing grounds used by the commercial fleet. In phase 4, the efficiency of the optimal vent design was tested on a commercial lobster vessel during normal trapping operations.

Modifications of the original experimental design were necessary because of changes in the fishery and its management while the experiment was being conducted. Beginning in 1983–1984, fishermen began replacing their old 50 × 100-mm wire-mesh traps with a new, smaller-mesh trap made of polyethylene, which led to an enormous

increase in slipper lobster catch in 1984–1985. Because of the increasing importance of the slipper lobster catch, we modified our vent design in 1985. Carapace length (CL) of the lobster was measured prior to 1986 to determine legal size. A minimum tail-width criterion was established in October 1985 in response to the increasing practice by commercial fishermen of detaching tails and freezing them at sea. This conversion from CL to TW also dictated a change in vent size. For ease of presentation, measurements originally recorded in CL have been converted to TW by the functional linear regressions $TW = 5.624 + 0.591CL$ ($N = 1,354$, $r^2 = 0.866$) for spiny lobsters and $TW = -2.106 + 0.779CL$ ($N = 1,655$, $r^2 = 0.953$) for slipper lobsters. Several changes in the minimum-size regulation for spiny lobster that occurred during our study, plus the establishment of a minimum legal size for slipper lobster (June 1987), required us to test a wider range of vent sizes than originally planned.

Laboratory experiments.—Gear selectivity studies with spiny lobsters (Bowen 1963; Paul 1984) indicated that a rectangular vent 285 mm wide and 54–60 mm high would be the optimal starting point for phase 1. Initially, at least five live spiny lobsters in each 1-mm size-class from 49 to 52 mm TW were obtained from commercial fishermen. The tips on the pleura of the abdominal tail segments were clipped in a predetermined pat-

tern to allow rapid identification of each size-class. These animals were passed through Plexiglas¹ vents with vertical dimensions of 54, 56, and 58 mm, and total escapement of each size-class was compared for all three vent sizes. The same experimental procedure was later used to determine the initial optimal circular-vent sizes for spiny and slipper lobsters.

Laboratory escapement trials were conducted in a U-shaped concrete enclosure with flowing seawater maintained at a depth of approximately 1 m. The tank was subdivided with wire mesh, and each test section was covered with a panel composed of heavy greenhouse shading material to protect the animals from the blinding effects of the sun (Phillips et al. 1980). In addition, concrete blocks provided shelter for the animals as they left a trap.

The Fathoms Plus shellfish trap, which by 1984 had almost completely replaced the wire-mesh trap originally used in the fishery (Figure 2), was used in laboratory trials. This dome-shaped, single-chambered trap is molded of black polyethylene, measures 980 × 770 × 295 mm, and has a mesh size of 45 × 45 mm (inside dimensions). Each trap has two entrance cones located on opposite sides.

The rectangular-vent panel was originally manufactured out of 18-gauge (1.3 mm) sheet aluminum. Thickness was increased to 11 gauge (3.2 mm) soon after the trials began, when it was discovered that the animals could pry their way out of the thinner models by bending the sides of the vent. Two vents, 285 mm wide and attached on opposite sides of the trap, were used in all trials, although their height and placement varied.

Laboratory trials (phase 2) in May 1984 tested vents with heights of 54, 55, and 56 mm, based on a legal size of 51 mm TW for spiny lobsters. These vents were placed on the sides of the traps 45 mm from the bottom (LOC I). To determine the effect of vent location on escapement of slipper lobsters, additional laboratory trials in June 1985 tested 55-mm vents placed at three other positions on the trap: 115 mm from the bottom (LOC II), 195 mm from the bottom (LOC III), and on the top of the trap (LOC IV) (Figure 2). A fourth trap, with vents placed at LOC I, served as a control. Reduction in minimum legal size of spiny lobsters to 47 mm TW prompted the repetition of the procedure in September 1985 with either 50- or 51-mm vents placed at LOC III.

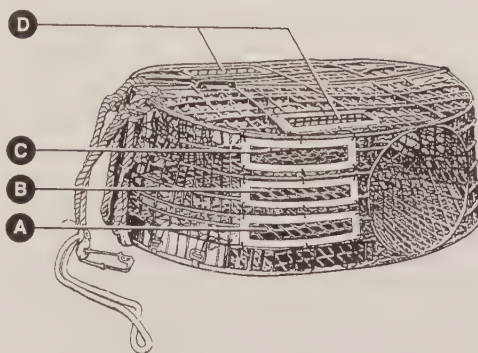


FIGURE 2.—Fathoms Plus shellfish trap, showing vertical placement of escape vents used to test for differences in escape rate: (A) 45 mm from bottom (LOC I); (B) 115 mm from bottom (LOC II); (C) 195 mm from bottom (LOC III); (D) top of trap (LOC IV).

Laboratory trials were conducted in March 1986 to compare escapement from circular and from rectangular vents for both species. In addition square vents were tested. The trials used three spiny lobsters in each 1-mm size-class from 47 to 52 mm TW and three slipper lobsters in each 5-mm size-class from 45 to 60 mm TW. All vents were placed at LOC I and on opposite sides; their sizes were as follows: (1) two rectangular (53 × 285-mm) vents (control); (2) two vent plates each containing three squarish (55 × 68-mm) vents placed in a row 25 mm apart; (3) two vent plates each containing three circular vents (70 mm in diameter) placed in a row about 25 mm apart.

Research vessel experiments. Initial *in situ* trials (phase 3) were conducted aboard the *Townsend Cromwell* over 13 d in June and October 1984. The traps used in the trials had two rectangular vents (12-gauge sheet aluminum) 54, 55, or 56 mm high. Six strings, with 10 traps per string, were set at various locations around Necker Island (June, October) and Maro Reef (October) at depths of 30–60 m. Each of the three vent sizes was fished on separate strings, and each string contained five vented traps alternated with five nonvented traps. Each trap was baited with chub mackerel *Scomber japonicus* and set shortly before sunset. Traps were hauled after 0800 hours the following morning, and all lobsters caught were weighed to the nearest 0.01 kg, measured (CL in mm), and sexed. Similar trials were conducted at the same locations in November 1985 to evaluate the effect of vent location on slipper lobster escapement. The same basic string configuration was used, except only 51 ×

¹ Reference to trade names does not imply endorsement by the U.S. National Marine Fisheries Service.

285-mm rectangular vents were tested. Nine strings of 12 traps each were set per day. The traps were arranged on the string in triplets that alternated traps with vents placed at LOC I, control traps (nonvented), and traps with vents at LOC III.

Commercial vessel experiments.—Commercial trials (phase 4) conducted aboard the fishing vessel *Shaman* from August to November 1986 compared the efficiencies of rectangular and circular vents in releasing sublegal slipper and spiny lobsters. Four rectangular (heights, 43, 45, 47, and 49 mm) and four circular (diameters, 60, 62, 65, and 67 mm) vent sizes were selected to provide a range of retention sizes that covered the 1986 50-mm TW minimum-size limit for spiny lobsters and the proposed 52–56-mm TW minimum-size limits for slipper lobsters. All panels were manufactured of 12-gauge aluminum plate cut into 335 × 113-mm rectangles. The circular vent consisted of four equal-sized holes spaced evenly across the panel (Figure 3) and mounted at LOC I, whereas the rectangular panel had the same configuration as previous models mounted at LOC III. All traps had a mesh size of 16 × 45 mm, a size reduction instituted by the manufacturer in 1986.

The *Shaman* typically set 6–12 strings with 50–200 traps per string, for a total of 1,100 traps/d. Experimental traps were arranged on the string as triplets spaced 50 m apart and consisting of a rectangular vented trap, a nonvented control trap, and a circular vented trap. Theoretically, this modified experimental design would reduce much of the variation in catch per trap along the string and between traps on different strings that might occur during commercial trapping operations. To facil-

itate comparison of catch rates of the two vent types with similar retention sizes, the smallest rectangular (43-mm) and smallest circular (60-mm) vents were fished in the same triplet, followed by consecutively larger vents of both configurations. Fishing effort with these traps totaled 1,800 trap-nights at Maro Reef, Gardner Pinnacles, Raita Bank, and Brooks Bank (Figure 1). Fishing effort was measured by comparing catch per unit effort (CPUE) defined as catch per trap-night. Typical soak times for the research vessel and commercial fishery trials averaged 12–15 h/d.

Results

Laboratory Experiments

Phase 1 laboratory trials established that 54-, 55-, and 56-mm rectangular vent heights were of the optimum range to allow escapement of sublegal (<77 mm CL) spiny lobsters. A second-degree response-surface model based on Andrew's sine robust procedure was applied:

$$ER = [\sin(b_0 + b_1 CL^2 + b_2 VS^2 + b_3 CL \cdot VS)]^2;$$

ER = escapement rate,

$b_0 = -1.39564$,

$b_1 = 0.0209091$,

$b_2 = 0.0446067$,

$b_3 = -0.0607644$,

CL = carapace length (mm),

VS = vent size (mm, vertical).

This model provided the best estimate of the parameter values and the rates of escapement at different vent sizes. Estimated escapement rates were calculated from the response-surface formula based upon results of phase 2 (Figure 4).

The phase 2 laboratory trials in June 1985 demonstrated that a rectangular vent 55 mm high placed at LOC III was most effective in deterring slipper lobster escapement without greatly influencing the escape of spiny lobster. The rate of slipper lobster escapement for this vent position, averaged over five trials, was 51% of the total number of slipper lobsters tested, compared with 85–98% for the other three vent positions. Similar results were obtained for spiny lobsters at the reduced minimum legal size of 47 mm TW.

The final set of laboratory trials suggested that, when circular vents 70 mm in diameter were used, escapement was similar for sublegal lobsters of both species. Total slipper lobster escapement was highest in traps fitted with a rectangular control vent and lowest in traps with circular vents. A similar number of spiny lobsters escaped from both

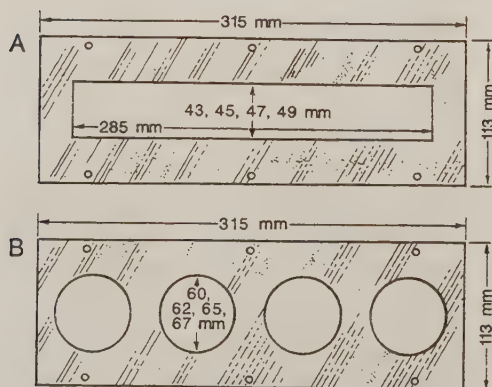


FIGURE 3.—Escape vent panels used during trials conducted aboard the commercial fishing vessel *Shaman*. (A) rectangular vent; (B) circular vents.

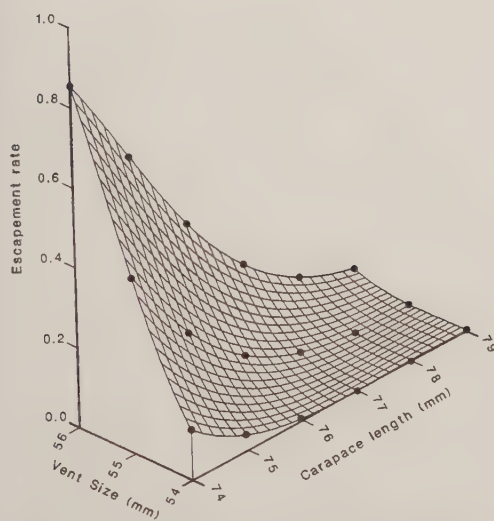


FIGURE 4.—Estimated escapement rate (expressed as a proportion) by rectangular vent size (vertical dimension) and carapace length for the initial spiny lobster laboratory trials in May 1984. Observed data points are indicated by black dots.

of these trap types. Square vents allowed escape-ment similar to that of circular vents for slipper lobsters from 53 to 56 mm TW; however, larger slipper lobsters continued to escape through the square vents by turning sideways and maneuvering through the square opening. Circular vents prevented this from occurring, indicating they could

be used to select for specific sizes of slipper lobsters based upon carapace width.

Research Vessel Experiments

The first series of in situ trials in June 1984 at Necker Island demonstrated that a 55-mm rectangular vent was most effective in allowing sub-legal (<51 mm TW) spiny lobster escapement without negatively affecting legal catch. Catches of legal spiny lobsters increased in traps fitted with vents (Table 1). Mean legal CPUE was highest, and sublegal CPUE was lowest, for spiny lobsters in traps equipped with 55-mm vents during trials in June and October 1984. In addition, the mean difference in CPUE of legal spiny lobsters in June 1984 was significantly higher for vented than for control traps (paired *t*-test, $P < 0.05$).

Retention curves comparing cumulative percentage of total catch with TW for June 1984 showed a decrease in catch of sublegal spiny lobsters for all three vented traps (Figure 5). Vented traps also tended to catch larger animals than control traps (Figure 5). Sublegal spiny lobsters equaled nearly 80% of the catch in control traps but less than 20% in each vented trap. Differences in sub-legal catches between control and vented traps were not as pronounced in October 1984 (Table 1) because of reductions in catch rates due to rough seas and poor weather conditions. However, despite poor catch rates, retention of sublegal spiny lobsters was reduced without significant escapement of legal animals.

TABLE 1.—Spiny lobsters: mean catch per unit effort (CPUE in trap hauls), standard error (SE), and mean difference in CPUE between rectangular-vented (V) and control (Con) traps (nonvented) during *Townsend Cromwell* cruises conducted in 1984 and 1985 for legal (≥ 51 mm tail width) and sublegal spiny lobsters. *N* = number of trap pairs (June and October 1984) or number of triplets (November 1985). For paired *t*-tests, asterisks denote $P < 0.05^*$ or $P \leq 0.01^{**}$.

Vent size (mm) ^a	N	Legal CPUE			Sublegal CPUE		
		V (SE)	Con (SE)	V - Con (SE)	V (SE)	Con (SE)	V - Con (SE)
June 1984							
54	77	1.54 (0.17)	1.12 (0.15)	0.42 (0.17)*	0.26 (0.06)	3.21 (0.56)	-2.95 (0.54)**
55	76	1.94 (0.23)	1.40 (0.21)	0.54 (0.25)*	0.14 (0.04)	3.40 (0.58)	-3.26 (0.58)**
56	80	1.27 (0.19)	1.01 (0.13)	0.26 (0.16)	0.25 (0.06)	3.28 (0.45)	-3.13 (0.44)**
October 1984							
54	170	0.82 (0.13)	0.88 (0.15)	-0.05 (0.11)	0.16 (0.03)	0.99 (0.23)	-0.84 (0.23)**
55	170	1.01 (0.14)	1.13 (0.20)	-0.12 (0.13)	0.03 (0.02)	0.93 (0.20)	-0.90 (0.19)**
56	170	0.94 (0.15)	1.08 (0.17)	-0.14 (0.14)	0.10 (0.04)	0.97 (0.21)	-0.87 (0.21)**
November 1985							
51 ^b	393	2.54 (0.24)	2.20 (0.21)	0.34 (0.14)*	1.34 (0.19)	3.63 (0.50)	-2.29 (0.34)**
51 ^c	392	2.59 (0.25)	2.18 (0.21)	0.41 (0.15)**	1.55 (0.21)	3.59 (0.50)	-2.04 (0.32)**

^a Vertical dimension.

^b LOC I: vent located 45 mm from bottom of trap.

^c LOC III: vent located 195 mm from bottom of trap.

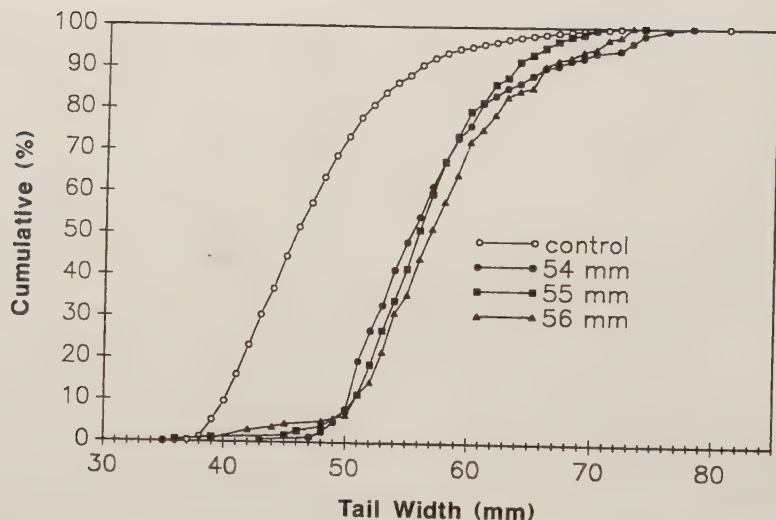


FIGURE 5.—Retention curves comparing cumulative percentage of total spiny lobster catch for rectangular-vented (54, 55, and 56 mm, vertical dimension) and control (unvented) traps tested in June 1984.

Field trials in November 1985 established that traps with 51-mm rectangular vents caught 50% more slipper lobsters when vents were at LOC III than when they were at LOC I (Table 2). However, the control trap without a vent outfished the LOC III trap by nearly 2.5 times for slipper lobsters larger than 50 mm TW (Table 2). Size-frequency distribution of slipper lobsters (LOC I: mean TW = 63.0 mm, SD = 4.50; LOC III: mean TW = 62.7 mm, SD = 5.24) was not significantly different for either vent location (Kolmogorov-Smirnov test, $D_{\max} = 0.0765$, $P > 0.05$). Catches of legal and sublegal spiny lobsters were similar for both vent locations (Table 1).

Commercial Vessel Experiments

Commercial trials aboard the *Shaman* suggested little difference in catch (mean difference in CPUE) of legal (≥ 50 mm TW) spiny lobsters between the vented (rectangular and circular) and control traps for the three smallest vent pairs tested (Table 3). However, traps fitted with the largest rectangular vents (49 mm) caught significantly greater numbers of legal spiny lobsters than the control traps (paired t -test, $P < 0.05$).

The relative catch of sublegal spiny lobsters, expressed as the mean difference in CPUE of vented traps minus the mean CPUE of the control traps,

TABLE 2.—Slipper lobsters: mean catch per unit effort (CPUE in trap hauls), standard error (SE), and mean difference in CPUE between rectangular-vented (V) and control (Con) traps (unvented) during *Townsend Cromwell* cruises in June 1984 and November 1985. N = number of trap pairs (June 1984) or number of triplets (November 1985). LOC I = vent located 45 mm from bottom of trap; LOC III = vent located 195 mm from bottom of trap. For paired t -tests, asterisks denote $P < 0.01^{**}$.

Vent size (mm) ^a	N	Mean CPUE		
		V (SE)	Con (SE)	V - Con (SE)
June 1984				
54	77	0.63 (0.14)	2.89 (0.23)	-2.26 (0.40)**
55	76	0.34 (0.09)	2.52 (0.36)	-2.18 (0.32)**
56	80	0.39 (0.12)	2.74 (0.29)	-2.35 (0.24)**
November 1985				
51 (LOC I)	393	0.73 (0.09)	3.40 (0.39)	-2.67 (0.32)**
51 (LOC III)	392	1.14 (0.15)	3.37 (0.38)	-2.23 (0.29)**

^a Vertical dimension

^a Vertical dimension.

TABLE 3.—Spiny lobsters: mean catch per unit of effort (CPUE), standard error (SE), and mean difference in CPUE between trap types within triplets (N) consisting of rectangular-vented (R), circular-vented (C), and nonvented control (Con) traps for legal (≥ 50 mm tail width) and sublegal spiny lobsters caught during commercial escape vent trials aboard the fishing vessel *Shaman*. For paired t -tests, asterisks denote $P < 0.05^*$ or $P < 0.01^{**}$.

Vent size (mm) ^a			Mean CPUE			Difference in CPUE	
R	C	N	R (SE)	Con (SE)	C (SE)	R - Con (SE)	C - Con (SE)
Legal lobsters							
43	60	457	0.96 (0.06)	1.03 (0.05)	1.03 (0.05)	-0.06 (0.07)	0.00 (0.07)
45	62	340	0.80 (0.05)	0.74 (0.05)	0.86 (0.05)	0.06 (0.06)	0.11 (0.07)
47	65	338	0.66 (0.06)	0.66 (0.05)	0.76 (0.05)	0.00 (0.08)	0.10 (0.07)
49	67	627	1.34 (0.06)	1.18 (0.05)	1.30 (0.06)	0.16 (0.07)*	0.12 (0.07)
Sublegal lobsters							
43	60	457	0.36 (0.04)	0.46 (0.06)	0.32 (0.04)	-0.09 (0.05)	-0.14 (0.06)**
45	62	340	0.16 (0.02)	0.23 (0.04)	0.19 (0.03)	-0.07 (0.04)	-0.04 (0.04)
47	65	338	0.37 (0.04)	0.64 (0.08)	0.17 (0.03)	-0.27 (0.08)**	-0.47 (0.08)**
49	67	627	0.51 (0.04)	1.75 (0.11)	0.29 (0.02)	-1.23 (0.11)**	-1.46 (0.11)**

^a Vertical dimension.

decreased with increasing vent size (Table 3). Significant (paired t -test, $P < 0.01$) results were obtained for the two largest vent pairs tested. The greatest mean difference in sublegal catch was attained with the 67-mm circular vent. This analysis clearly showed the increased efficiency of vented traps in releasing sublegal lobsters as vent size increased.

The mean difference in CPUE of legal slipper lobsters (≥ 56 mm TW) generally increased with vent size for the first three sizes of rectangular and circular vent pairs (Table 4; Figure 6). Traps equipped with the largest rectangular vent (49 mm) caught significantly fewer legal slipper lobsters than did adjacent control traps (paired t -test, $P < 0.01$). However, mean difference in legal slipper lobster CPUE for 67-mm circular vented traps versus control traps was not significant ($P > 0.05$). Sim-

ilar results were observed when the minimum legal size for slipper lobsters was assumed to be either 54 or 52 mm TW.

Both circular and rectangular vented traps reduced catch of sublegal slipper lobsters for the aforementioned minimum legal sizes examined. Mean differences in sublegal CPUE between vented and control traps generally increased as the size of the vent pairs increased, except for the largest rectangular (49 mm) and circular (67 mm) vent pairs. However, differences were still highly significant (paired t -test, $P < 0.01$). When these mean differences were expressed as percentages of the control CPUE, these percentages decreased with decreasing vent size (Figure 6). The 67-mm circular and 49-mm rectangular vented traps caught over 90% fewer sublegal slipper lobsters than did their respective controls. Retention of sublegal

TABLE 4.—Slipper lobsters: mean catch per unit effort (CPUE), standard error (SE), and mean difference in CPUE between trap types within triplets (N) consisting of rectangular-vented (R), circular-vented (C), and nonvented control (Con) traps for legal (≥ 56 mm tail width) and sublegal slipper lobsters caught during commercial escape vent trials aboard the fishing vessel *Shaman*. For paired t -tests, asterisks denote $P < 0.01^{**}$.

Vent size (mm) ^a			Mean CPUE			Difference in CPUE	
R	C	N	R (SE)	Con (SE)	C (SE)	R - Con (SE)	C - Con (SE)
Legal lobsters							
43	60	354	0.62 (0.05)	0.64 (0.06)	0.73 (0.06)	-0.03 (0.06)	0.08 (0.06)
45	62	486	1.84 (0.13)	1.93 (0.13)	2.06 (0.14)	-0.09 (0.11)	0.13 (0.10)
47	65	504	3.71 (0.18)	3.52 (0.19)	3.66 (0.18)	0.19 (0.14)	0.14 (0.15)
49	67	315	0.50 (0.05)	0.74 (0.08)	0.67 (0.07)	-0.24 (0.07)**	-0.07 (0.09)
Sublegal lobsters							
43	60	354	0.29 (0.03)	0.56 (0.05)	0.45 (0.05)	-0.27 (0.05)**	-0.11 (0.06)
45	62	486	0.40 (0.03)	0.93 (0.05)	0.64 (0.05)	-0.53 (0.06)**	-0.3 (0.06)**
47	65	504	0.59 (0.05)	2.54 (0.13)	1.13 (0.07)	-1.95 (0.12)**	-1.41 (0.11)**
49	67	315	0.03 (0.01)	0.43 (0.04)	0.03 (0.01)	-0.40 (0.04)**	-0.40 (0.04)**

^a Vertical dimension.

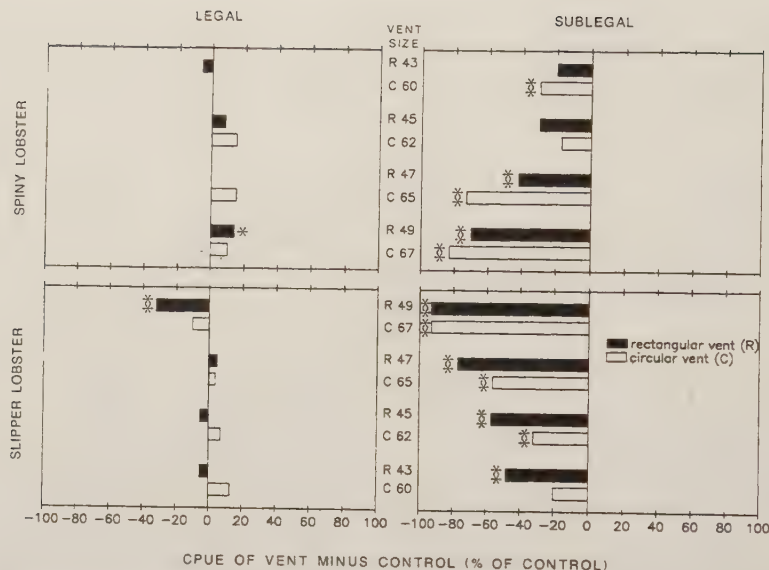


FIGURE 6.—Histograms of mean catch per unit effort (CPUE) of vented traps minus mean CPUE of control (unvented) traps, expressed as a percentage of control trap CPUE for spiny and slipper lobsters caught during commercial trials aboard the fishing vessel *Shaman*, August–November 1986. Rectangular (R) and circular (C) vent sizes are vertical dimensions (mm). For paired *t*-tests, asterisks denote $P < 0.05^*$ or $P < 0.01^{**}$.

lobsters was substantially less in traps with either vent type compared with the control traps (Figure 7).

Circular vents performed better than rectangular vents in maximizing combined escapement of sublegal lobsters of both species while minimizing loss of legal lobsters. To achieve sublegal escapement from rectangular traps that is 70% higher than the escapement from control traps, 49-mm rectangular vents must be used (Figure 6). This vent size also significantly reduced legal slipper lobster CPUE by 32% (paired *t*-test, $P < 0.01$). However, if a smaller rectangular vent was used, sublegal spiny lobster retention increased dramatically. In contrast, a 67-mm-diameter circular vent provided 83% and 93% reduction in catches of sublegal spiny and slipper lobsters, respectively, compared with those of the control traps (Figure 6). The 67-mm circular vents also allowed 10% more sublegal spiny lobsters to escape, compared with the 49-mm rectangular vents, and they reduced escapement of slipper lobsters larger than 56 mm TW (Figure 7).

Discussion

The use of escape vents substantially reduces the catch of sublegal lobsters and, compared with

traps without vents, often increases the catch of legal animals. This trend was evident for both vent designs and both species. Researchers working in other lobster fisheries throughout the world have also reported substantial reductions in retention of sublegal lobsters and increases in legal catches with vented traps (Everson 1986). In Western Australia, an area with one of the largest lobster fisheries in the world (Brown and Caputi 1983), vented traps have been used successfully since 1966. During vent trials in the Abrolhos Islands, Bowen (1963) found that traps with 57-mm rectangular vents caught at least 54% fewer sublegal rock lobsters *Panulirus cygnus*, compared with nonvented traps, while actually increasing legal catch. Similar results were reported by Ritchie (1966) and Bain (1967), prompting vent legislation for the spiny lobster fishery in New Zealand.

Escape vents have been required in lobster traps used in California since 1957. Recently, vent size was increased from 51 to 60 mm, resulting in a 75% reduction in sublegal catch and a steady increase in legal catch (K. Miller, California Department of Fish and Game, unpublished data presented at the California Cooperative Oceanic Fishery Investigation Conference, 1985). A similar situation exists in the Maine fishery for the

American lobster *Homarus americanus*. Vent experiments conducted by the Rhode Island Division of Fish and Game confirmed that vented traps reduce the catch rate of sublegal lobsters by 79% and also consistently catch more legal lobsters (Fogarty and Borden 1980). Vented traps are now required in all lobster-producing states throughout New England.

The mechanism allowing for escape of sublegal lobsters from vented traps is straightforward. Animals enter the traps to feed on bait and then leave through the vent opening once they become satiated or all the bait is consumed (Ritchie 1966). More difficult to explain are observations by many researchers that vented traps often produce a greater legal catch. This phenomenon is likely due to a combination of several behavioral interactions between size-classes and species. In the New England fishery, Fogarty and Borden (1980) noted that non-vented traps often reach a saturation point that prevents additional lobsters from entering. Vented traps allow sublegal animals to escape, allowing more legal lobsters to enter. Interspecific and intraspecific competition resulting in a size-dependent hierarchy also may be a factor. Large *Jasus* spp. often drive smaller individuals from traps through the vent openings (Ritchie 1966).

The circular vent is unique in that it allows sublegal lobsters from different taxonomic families and with dramatically dissimilar body dimensions to escape in nearly equal proportions. The basis for this lies in the ability of a circular vent to select for carapace width as well as height, whereas rectangular designs merely select for height. Hence, the wider, flatter slipper lobster can escape in greater quantities than the rounder spiny lobster. Krouse (1978) also reported this phenomenon in a study of the effect of escape vent shape on catches of American lobsters and rock crabs *Cancer* spp. in the Maine fishery. He found that circular vents selected for lobsters, of similar size as those retained by rectangular vents, but also retained marketable-size crabs.

Another important consideration was the total vent area available for escapement. While testing different vent configurations in Hawaii, Paul (1984) concluded that configurations with the greatest total vent area provided the most escapement. A similar observation was made by Ritchie (1966) during vent experiments conducted aboard commercial fishing boats in New Zealand. Fogarty and Borden (1980) observed in the laboratory that lobsters located vent openings by a random process and that larger target areas were located more

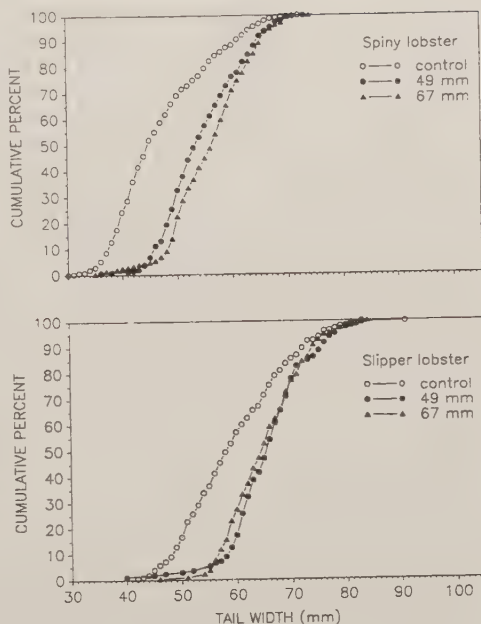


FIGURE 7.—Retention curves comparing cumulative percent caught for 67-mm circular-vented traps, 49-mm (vertical dimension) rectangular-vented traps, and control traps (unvented) for spiny and slipper lobsters caught during commercial trials aboard the fishing vessel *Shaman*, August–November 1986.

quickly and efficiently. Moreover, Brown and Caputi (1986) found that, by increasing vent height by 1 mm and doubling the number of vents per trap from one to two, they decreased retention of sublegal rock lobsters an additional 40–60% without affecting legal catch. These results and our own observations demonstrate the importance of having two vent panels, rather than one, in each trap.

Escape vents provide an inexpensive way of diminishing sublegal mortality caused by handling, which can have a major effect on future recruitment in many fisheries (Krouse and Thomas 1975; Lyons and Kennedy 1981; Brown and Caputi 1983, 1985, 1986; Hunt and Lyons 1986; J.J.P., unpublished report). Fishery-induced injuries can also significantly affect yield by slowing growth and thus delaying entry into the legal fishery (Davis 1981). Properly fitted escape vents reduce the risk of these injuries (Brown and Caputi 1983). An added benefit resulting from the use of vents is the reduction in catch-handling time (Brown and Caputi 1985).

The evidence is overwhelmingly in favor of the use of escape vents in lobster fisheries in Hawaii

and throughout the world. Because of our results, circular escape vents 67 mm in diameter have been required in all lobster traps used in the northwestern Hawaiian Islands after 1 January 1988. Commercial logbook catch statistics for spiny and slipper lobsters revealed that the percentage of sublegal spiny lobsters in the catch decreased from 32% to 22% in 1987 (Clarke, unpublished data). Reduction in the sublegal spiny lobster catch was most pronounced at Necker Island (42 to 26%), which historically has produced large catches of sublegal lobsters (Figure 8). These 1988 figures amount to 32% and 38% reductions in sublegal spiny lobster catch relative to the previous year for all banks combined and for Necker Island, respectively. The observed sublegal catch was the lowest reported for the fishery since implementation of the Fishery Management Plan in 1983 (Figure 9) (Clarke, unpublished data). Total legal spiny lobster CPUE rose from 0.49 per trap-haul in 1987 to 1.05 in 1988. Following implementation of the minimum-size regulation, 25% of the slipper lobster catches were sublegal. Although there may be many reasons for apparent changes in catch composition in a fishery (J.J.P., unpublished report), these most recent commercial catch figures substantiate the effectiveness of escape vents.

The final judgment, of course, rests with the fishermen. Initial resistance has given way to popular acceptance in many of the fisheries in which vents are used (Everson 1986). During our study, the final phase of the vent experiment was conducted aboard a commercial vessel, giving the crew a firsthand experience with the effectiveness of

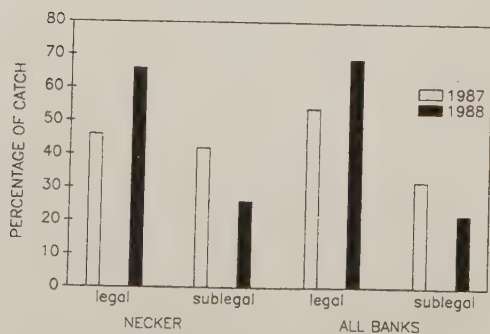


FIGURE 8.—Legal-sublegal composition (in percentages) of the commercial catch of spiny lobsters in the northwestern Hawaiian Islands, 1987–1988, based on unpublished logbook data of R. P. Clarke, National Marine Fisheries Service. Totals do not include catch of berried lobsters.

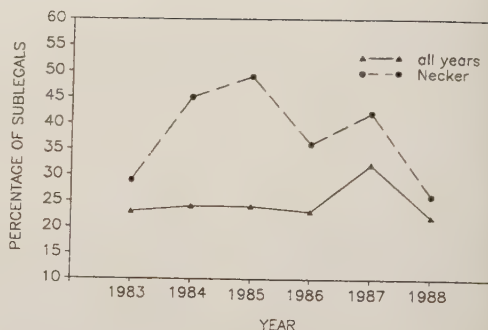


FIGURE 9.—Percentages of sublegal spiny lobsters caught by year in the northwestern Hawaiian Islands, 1983–1988, based on unpublished logbook data of R. P. Clarke, National Marine Fisheries Service.

vents. Even so, other fishermen were initially hesitant to accept the benefits of vents. Widespread acceptance did not occur until after the vent regulation became law and the first catches by vented traps were landed.

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This study would not have been possible without assistance and helpful suggestions from many members of the commercial lobster fishery in Hawaii. We especially thank the owners, captains, and crews of the fishing vessels *Shaman* and *Lusty*. J. Hebert must be singled out for convincingly advocating the use of circular vents. Several of our coworkers at the Honolulu Laboratory of the National Marine Fisheries Service were instrumental in the development and completion of this project. R. Clarke and T. Kazama collected all of the data aboard the *Shaman*, and L. Tsukano spent countless hours overseeing data entry. S. Ralston, D. Tagami, R. Benco, and G. Kamer provided invaluable help with data analysis. We also thank all of the reviewers for their helpful comments.

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Cardiac physiology in tunas. I. *In vitro* perfused heart preparations from yellowfin and skipjack tunas

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An *in situ* heart preparation perfused with oxygenated saline was used to examine cardiac performance at 25°C in yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*). Heart rates (91–172 bpm in skipjack tuna and 101–157 bpm in yellowfin tuna) were comparable to those measured *in vivo*, and physiological stroke volumes were possible in yellowfin tuna with subambient filling pressures. In yellowfin tuna, maximum stroke volume and cardiac output were similar to the values obtained *in vivo* with spinally blocked animals; mean output pressures (up to 145 cmH₂O, 1 cmH₂O = 0.098 kPa) could exceed *in vivo* values without a major decrease in the resting cardiac output (homeometric regulation). In contrast, saline-perfused skipjack tuna hearts could not develop physiological output pressures without compromising cardiac output, with cardiac output being only 63% of the *in vivo* value at an output pressure near the *in vivo* ventral aortic pressure. The poor performance of the skipjack tuna heart is attributed to limited oxygen diffusion through the thicker walled ventricle. We conclude that the tuna heart is more dependent on its coronary circulation for normal function than the hearts of other fishes examined thus far. The coronary circulation was perfused with saline at various flow rates in isolated hearts from skipjack tuna to develop a pressure–flow relationship for the intact circulation. Coronary resistance reached a minimum of 24 cmH₂O · min · g ventricular mass/mL at a flow rate of 2 mL/(min · g ventricular mass) with perfusion pressure about 40 cmH₂O. *In vivo* coronary blood flow was estimated from the pressure–flow relationship as 0.67 mL/(min · g ventricular mass). Injections of adrenaline, noradrenaline, and phenylephrine into coronary circulation under constant flow conditions increased perfusion pressure, indicating the possibility of α -adrenergic vasoconstriction.

FARRELL, A. P., DAVIE, P. S., FRANKLIN, C. E., JOHANSEN, J. A., et BRILL, R. W. 1992. Cardiac physiology in tunas. I. *In vitro* perfused heart preparations from yellowfin and skipjack tunas. *Can. J. Zool.* 70 : 1200–1210.

La perfusion *in situ* de coeurs de Thons à nageoires jaunes (*Thunnus albacares*) et de Thons à ventre rayé (*Katsuwonus pelamis*) au moyen d'une solution saline oxygénée a permis de mesurer la performance cardiaque de ces poissons à 25°C. Les rythmes cardiaques, 91–172 bpm chez le Thon à ventre rayé et 101–157 bpm chez le Thon à nageoires jaunes, étaient comparables à ceux enregistrés *in vivo* et des volumes systolaires physiologiques pouvaient être obtenus chez le Thon à nageoires jaunes en appliquant des pressions de remplissage sousambiantes. Chez le Thon à nageoires jaunes, le volume systolique maximal et le rendement cardiaque étaient semblables aux valeurs obtenues *in vivo* chez des poissons soumis à un blocage spinal; les pressions moyennes à la sortie du coeur (jusqu'à 145 cmH₂O, 1 cmH₂O = 0.098 kPa) pouvaient dépasser les valeurs *in vivo* sans qu'il y ait de chute importante du rendement cardiaque au repos (contrôle homéométrique). En revanche, les coeurs de Thons à ventre rayé en perfusion dans la solution saline ne pouvaient pas fournir de pressions physiologiques sans compromettre le rendement cardiaque et le rendement cardiaque n'était que de 63% de la valeur *in vivo* à une pression à peu près égale à la pression obtenue dans l'aorte ventrale *in vivo*. La mauvaise performance du coeur du Thon à ventre rayé est attribuable à une diffusion d'oxygène diminuée par l'épaisseur importante de la paroi du ventricule. Nous concluons que la circulation coronarienne a plus d'impact sur le bon fonctionnement du coeur chez les thons que chez tout autre poisson examiné précédemment. La perfusion du système coronarien dans une solution saline à diverses vitesses de circulation dans des coeurs isolés de Thons à ventre rayé a servi à établir la relation pression–vitesse de circulation qui permet une circulation intacte. La résistance coronarienne a atteint un minimum de 24 cmH₂O · min · g · masse ventriculaire/mL à une vitesse de circulation de 2 mL/(min · g masse ventriculaire) (environ 40 cmH₂O) ou plus. La vitesse de circulation du sang *in vivo* dans le système coronarien a été estimée à 0,67 mL/(min · g masse ventriculaire) à partir de la relation pression–circulation établie précédemment. Des injections d'adrénaline, de noradrénaline et de phényléphrine dans la circulation coronarienne dans des conditions constantes d'écoulement ont augmenté la pression de perfusion, ce qui indique la possibilité d'une vasoconstriction sous contrôle α -adrénergique.

[Traduit par la rédaction]

Introduction

Tunas are amongst the most athletic of fishes. Their metabolic rates are almost an order of magnitude greater than those of rainbow trout (*Oncorhynchus mykiss*), approaching those of similarly sized mammals (see Dizon *et al.* 1978; Brill 1987). Many tuna species have body temperatures higher than the

water in which they live (Carey 1973) as a consequence of specialized vascular countercurrent systems (Kishinouye 1923; Graham and Diener 1978) for conserving metabolic heat. Tunas generate higher arterial blood pressures than other fishes (Stevens 1972; Bushnell 1988) to drive blood through the relatively high vascular resistance of the branchial circulation (Muir and Brown 1971). Correspondingly, the relative heart mass in tunas is greater than in other fishes (Basile *et al.* 1976; Tota 1978; Poupa *et al.* 1981; Davie 1987). The ventricle has a thick layer of compact myocardium (>40% by mass; Santer and Greer-Walker 1980), and the coronary circulation supplies both the outer compact and inner spongy layers of myocardium (Tota *et al.* 1983; Tota 1989). The metabolic zonation between the compact and spongy layers has been

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characterized (Maresca *et al.* 1976; Tota 1978; Gemelli *et al.* 1980; Tota 1983).

Cardiac output values at 25°C for normoxic spinally blocked yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) are 115 and 132 mL/(min · kg), respectively (Bushnell 1988; Brill and Bushnell 1991). These values are more than double the maximum cardiac output and 6 times the resting cardiac output reported for rainbow trout at 10°C (17 mL/(min · kg), Kiceniuk and Jones 1977). Similarly, ventral aortic blood pressure in tunas (115–119 cmH₂O, 1 cmH₂O = 0.098 kPa) is about twice that in rainbow trout (53 cmH₂O, Kiceniuk and Jones 1977) and 3 times that in sea raven (*Hemirhamphus intermedius*) (42 cmH₂O, Farrell 1986). Heart rates, measured in spinally blocked yellowfin tuna and skipjack tuna, are 97 and 126 beats per minute (bpm), respectively, and at these heart rates, stroke volumes are 1.3 mL/kg for yellowfin tuna and 1.1 mL/kg for skipjack tuna (Bushnell 1988). Maximum heart rates have been measured at 180–210 bpm in swimming tunas (Kanwisher *et al.* 1974; Bushnell 1988). The maximum heart rate reported in other lower vertebrates (fishes, amphibians, and reptiles) apparently does not exceed 120 bpm (Farrell 1991). Because the tuna heart clearly outperforms hearts of other fishes, we were particularly interested in increasing our knowledge of tuna cardiac physiology.

Our experimental approach for this study used an *in situ* perfused heart preparation. *In situ* perfused heart preparations have been used previously with a variety of fish species, providing useful information on the control of stroke volume and on the maximum capacity of the heart to generate flow and pressure (Farrell *et al.* 1983, 1985, 1988; Davie and Farrell 1991a). Rainbow trout hearts perfused with aerated perfusate and no coronary perfusion can perform work at levels comparable to the maximum *in vivo* level (Milligan and Farrell 1991). To provide additional information about the coronary circulation, pressure–flow relationships were determined by perfusing the coronary circulation of isolated skipjack tuna hearts with saline. In a companion study, the contractile properties of tuna cardiac muscle were examined with atrial strips isolated from skipjack tuna (Keen *et al.* 1992).

Materials and methods

Studies with *in situ* saline-perfused hearts

Data are reported for successful preparations from 10 skipjack tuna (mean body mass 1.32 ± 0.13 kg) and 8 yellowfin tuna (mean body mass 1.97 ± 0.08 kg). The fish were purchased from local fishermen and maintained in outdoor tanks at 24–25°C at the Kewalo Research Facility (Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, Hawaii).

In situ heart preparation

The *in situ* perfused preparation was based on that developed for the rainbow trout in which the pericardium was left intact (Farrell *et al.* 1988). The basic procedure involved the following steps. Fish were anaesthetized with MS-222 (1 g/L plus 0.3 g/L NaHCO₃) in seawater and maintained in an anaesthetized state on an operating sling by irrigating the gills with cooled (15–20°C) MS-222 (0.1 g/L plus 0.03 g/L NaHCO₃). Sodium heparin (10 000 IU) was injected into the caudal vessels to prevent blood clotting in the heart. The peritoneal cavity was opened with a ventral incision. The intestinal vessels were ligated and the stomach and intestine removed to provide easier access to the hepatic veins. Two hepatic veins drain into the sinus venosus. After tying off the more dorsal one, the central hepatic vein was cannulated with a large-bore stainless steel tube to locate the

tip of the cannula in the sinus venosus. This tube acted as an input cannula through which the heart received oxygenated saline at constant pressure from a Mariott bottle. Cardiac perfusion began immediately after the input cannula was secured. A gill arch was cut prior to opening the hepatic vessel, because air was aspirated into the heart chamber by its pumping action, and these air bubbles became trapped in the gill capillaries, creating a large back pressure on the heart. A large-bore stainless steel tube was secured in the ventral aorta to act as an output cannula. The ventral aorta was exposed in the isthmus region, and the cannula was advanced into the ventral aorta so that the tip was located in the region of the bulbus arteriosus. In some preparations the common cardinal veins were tied off. However, in later preparations this step was omitted because it reduced the volume of the sinus venosus. In all preparations the fish was transected near the pelvic fins so that the preparation could fit into the organ bath. In preparations in which the common cardinal veins were not tied off, a closed tube was inserted into the severed caudal vein. These surgical procedures lasted 10–20 min, after which the preparation was transferred to the organ bath. The preparation was fully immersed in saline at 25°C. The input cannula was connected to the perfusate reservoirs via an adjustable constant pressure device (Farrell *et al.* 1983) that set the filling pressure of the heart. The output cannula was connected to an adjustable constant pressure head that set the diastolic output pressure. Cardiac output was measured via an in-line, flow-through electromagnetic flow probe (Zepeda Instruments, Seattle, Wash.). The input and output pressures were continuously measured with U-Onics P-106 (Wayland, Mass.) pressure transducers that were connected to 23-gauge tubes which were inside the stainless steel cannulae and which opened at the orifice of the cannula.

Saline composition

The composition (in mM) of the saline used throughout this study was: 185.7 NaCl, 1.1 MgCl₂ · 6H₂O, 7.0 KCl, 1.9 CaCl₂ · 2H₂O, 7.1 N-tris[hydroxymethyl]methyl-2-aminoethanesulfonic acid (TES, Na salt), 2.8 TES (free acid), and 5.5 dextrose. The final pH at 25°C was 7.7. In previous studies with perfused hearts, tonic levels of adrenaline were found to be important in improving the durability of the preparation. Therefore, in the absence of other information for tunas regarding either perfused hearts or *in vivo* levels of adrenergic stimulation (neural or humoral), adrenaline was added to the saline to a final concentration of 0.1 µM. Aerated saline was used successfully with rainbow trout hearts in which the coronary circulation was not perfused (Farrell *et al.* 1988; Milligan and Farrell 1991). Moreover, rainbow trout hearts performed at work loads comparable to the maximum *in vivo* level for at least 40 min without deterioration, suggesting adequate oxygen delivery to the myocardium in the absence of coronary perfusion. The perfusate used in this study was oxygenated. Therefore, the partial pressure of oxygen (P_{O₂}) of the tuna perfusate was approximately 5 times higher than that used in successful rainbow trout hearts and approximately 20 times higher than that of tuna venous blood (30 mmHg, Bushnell 1988). We anticipated that this supernormal luminal P_{O₂} would compensate for the fact that the coronary circulation was not perfused. In some experiments lactate and fatty acids were added to the saline.

Instrumentation, calibrations, and data analysis

The flow probe was calibrated with known flow rates of saline. The pressure transducers were calibrated daily with a water manometer. Pressures were referenced to the saline in which the preparation was fully immersed. The pressure and flow signals were suitably amplified and displayed on a Gould chart recorder (Cleveland, Ohio). In addition, an A/D converter (ADDA12, Flytech), interfaced with an IBM AT computer, recorded these signals. Mean pressures, cardiac output, stroke volume, and heart rate were calculated from representative records taken over a 10-s period. Cardiac power output was calculated as follows:

$$\text{power output (mW)} =$$

$$\text{cardiac output (mL/s)} \times (P_o - P_i) \text{ (cm H}_2\text{O)} \times 0.098$$

where P_o is output pressure, P_i is input pressure, and 0.098 converts $\text{mL} \cdot \text{cmH}_2\text{O/s}$ to mW. Power output is expressed per unit body mass (kg) and per unit ventricular mass (g).

In some preparations, 1-mL saline samples were taken simultaneously from the input and output lines near the heart. The Po_2 in these samples was measured with a Radiometer PHM 73 analyzer (Copenhagen, Denmark) and associated oxygen probe maintained at 25°C . Some samples of perfusate were collected from the output head and used for analysis of lactate (Bergmeyer 1974).

Experimental protocols for yellowfin tuna

Diastolic output pressure was initially set to 60–70 cmH_2O , and the filling pressure in the sinus venosus was set so that cardiac output averaged 80–90 $\text{mL}/(\text{min} \cdot \text{kg})$. The beating frequency of the perfused heart was set by the intrinsic rate of the sino-atrial pacemaker plus the adrenergic tone provided by the adrenaline in the perfusate. Filling pressure was increased in a stepwise manner to generate a Starling curve for each preparation ($N = 8$). A maximum stroke volume was established when a further increase in filling pressure failed to produce an increase in cardiac output. With cardiac output at this maximum level, diastolic output pressure was increased in a stepwise fashion to examine homeometric regulation by the heart (i.e., the ability of the heart to intrinsically adjust pressure development without compromising flow development). Diastolic output pressure was raised until the heart failed, as indicated by a significant decrease in cardiac output ($N = 6$). A value for maximum power output was established during this procedure. Heart rate decreased to a stable level (the reported mean heart rate) at the outset of the experiment. Maximum heart rate refers to the highest heart rate observed at the beginning of the perfusion.

Experimental protocols for skipjack tuna

The same experimental protocol was attempted for the skipjack tuna with limited success. Data are reported for 10 skipjack tuna heart preparations that performed with a mean output pressure between 70 and 80 cmH_2O , which is near the *in vivo* ventral aortic blood pressure (Bushnell 1988). However, cardiac performance deteriorated rapidly in another 20 preparations. In most of these cases, cardiac output was reasonably high (30–80 $\text{mL}/(\text{min} \cdot \text{kg})$) provided that the diastolic output pressure was subphysiological (20–30 cmH_2O). Cardiac deterioration was greatly accelerated when diastolic pressure was increased to a physiological level. Increasing the adrenaline concentration in the perfusate to 1.0 μM did not attenuate the decline. When the pericardium was opened to view the heart in some of these failing preparations, it appeared as if only the atrium was contracting forcefully, with the atrium and ventricle beating at different rates.

Cardiac morphology

The ventricle and atrium were removed after the experiment, blotted on paper towelling, weighed, and fixed in formalin. Compact and spongy myocardial tissues were dissected from the formalin-fixed ventricle and dried to a constant mass. Compact myocardium is reported as a percentage of the ventricle mass.

Pressure–flow relationships for the coronary circulation

Six skipjack tuna (body mass 1.61 ± 0.12 kg) were used. Fish were either stunned by a blow to the head or anaesthetized by immersion in buffered MS-222 (1 g/L). Sodium heparin (10 000 IU) in 0.8 mL of saline was injected into the caudal vessels. The heart was quickly removed via a midventral incision through the pericardial wall and was placed in a dish of ice-chilled saline. Care was taken not to tear the atrium when cutting through the sinus venosus. A PE 50 cannula (i.d. = 0.58 mm, o.d. = 0.97 mm, Clay Adams) was secured in the single coronary artery that lies on the dorsal surface of the ventral aorta. Ten millilitres of heparinized saline (1000 IU/mL) was injected from a syringe into the coronary artery to help clear the coronary circulation of blood and prevent clotting. The cannulated heart was immersed in saline at 25°C for the perfusion studies. Preparation time was approximately 10 min.

The coronary circulation was perfused with saline (see above) under constant flow conditions using a Haake MP2000 peristaltic

pump (New Jersey). A windkessel was placed in the inflow line to reduce the large pressure oscillations produced by the pump (Farrell 1987). Perfusion (input) pressure was monitored by a sidearm in the input cannula connected to a U-Onics P106 pressure transducer (Wayland, Mass). Perfusion pressure was referenced to the saline in the organ bath and corrected for the flow-dependent pressure drop along the input cannula, downstream from the measurement site. The cannula resistance was determined at the end of each experiment by measuring the pressure drop at two known flow rates. The suture around the cannula was left in place for this calibration procedure. The pressure signal was suitably amplified and displayed on a Gould chart recorder (Cleveland, Ohio).

Experimental protocol

Flow was initially set at 0.5 $\text{mL}/(\text{min} \cdot \text{kg body mass})$ to clear blood from the preparation and establish a stable perfusion pressure. The heart was not beating. Pressure–flow curves were generated by measuring stable perfusion pressures at 14 flow rates ranging from 0.01 to 3 $\text{mL}/(\text{min} \cdot \text{kg body mass})$. The highest flow rate represented approximately 3% of the resting cardiac output measured in spinally blocked skipjack tuna (Bushnell 1988).

Flow was then set to 1 $\text{mL}/(\text{min} \cdot \text{kg body mass})$ prior to measuring the effects of vasoactive drugs on the coronary circulation. Preparations were tested with no more than three vasoactive drugs, which were injected into the perfusion line as a bolus of 0.1 or 0.2 mL. Dose–response curves were established for L-adrenaline bitartrate, L-noradrenaline bitartrate, L-phenylephrine hydrochloride, DL-isoproterenol, acetylcholine hydrochloride, and adenosine diphosphate (ADP) (Sigma). Perfusion pressure returned to a stable level between successive drug injections. The maximum response to the drugs is presented as a percentage change from the initial coronary resistance.

Calculations

At the end of the experiment the ventricle was weighed and coronary flow rate was recalculated as $\text{mL}/(\text{min} \cdot \text{g ventricular mass})$. In the absence of information on the drainage of tuna coronary veins and coronary venous blood pressure, we assumed that coronary venous pressure was zero when calculating coronary vascular resistance. Coronary vascular resistance = (input pressure)/(coronary inflow), where resistance is in $\text{cmH}_2\text{O} \cdot \text{min} \cdot \text{g ventricular mass}/\text{mL}$, input pressure is in cmH_2O , and coronary inflow is in $\text{mL}/(\text{min} \cdot \text{g ventricular mass})$. An unknown proportion of the coronary circulation perfuses the spongy myocardium of the tuna heart and empties directly into the ventricle (Tota 1978; Tota 1983; Tota *et al.* 1983), but the effect of this anatomical arrangement on our calculations is unknown.

Mean values and standard error of the mean are presented. Statistical comparisons were made using a Student's *t*-test with the limit of significance set at $p < 0.05$.

Results

Cardiac morphology

The ventricular mass was $0.40 \pm 0.01\%$ of body mass in skipjack tuna and $0.29 \pm 0.01\%$ of body mass in yellowfin tuna (Table 1). This was a statistically significant species difference. The value for the relative ventricular mass of skipjack tuna is larger than previously reported values for tunas (northern bluefin tuna *Thunnus thynnus* (relative ventricular mass, 0.31% of body mass; Poupa *et al.* 1981) and southern bluefin tuna *Thunnus maccoyii* (relative ventricle mass, 0.29% of body mass; Davie 1987)). Other tunas, which were part of the physiological data set, had similarly sized ventricles. The compact layer of skipjack tuna hearts comprised a significantly greater proportion of the total ventricular mass ($65.6 \pm 1.2\%$) compared with yellowfin tuna ($54.5 \pm 1.2\%$). The estimates for compact myocardium are higher than other estimates for tunas using the same technique (e.g., 48.5% in southern

TABLE 1. Cardiovascular variables for skipjack and yellowfin tunas

	Skipjack tuna	Yellowfin tuna
Maximum cardiac output (mL/(min · kg body mass))	84.5 ± 5.4	108.0 ± 4.0
Maximum stroke volume mL/g ventricular mass	0.17 ± 0.01	0.31 ± 0.02
mL/kg body mass	0.68 ± 0.05	0.87 ± 0.10
Maximum sustainable output pressure (cmH ₂ O)		
Systolic	109.0 ± 4.1	178.5 ± 6.3
Mean	84.7 ± 4.0	145.1 ± 5.8
Maximum power output mW/g ventricular mass	2.55 ± 0.21	7.58 ± 0.44
mW/kg body weight	10.1 ± 0.88	21.9 ± 1.04
Mean heart rate (bpm)	138.5 ± 7.1	123.3 ± 4.2
Maximum heart rate (bpm)	154.0 ± 5.0	137.6 ± 4.8
Body mass (kg)	1.32 ± 0.13	1.96 ± 0.08
Heart mass (g)	5.22 ± 0.44	5.72 ± 0.30
Compact myocardium (%)	65.6 ± 1.23	54.5 ± 1.21
Relative ventricular mass	0.40 ± 0.01	0.29 ± 0.01
N	10	8

NOTE: Values are given as means ± SEM. Maximum cardiac output, maximum stroke volume, and mean heart rate values were obtained from the response to increasing filling pressure. Maximum output pressures and maximum power output values were obtained from the response to increased output pressure. Maximum heart rate was derived from the highest value observed for each preparation. Relative ventricular mass is ventricular mass expressed as a percentage of body mass. All the variables reported for the skipjack tuna were statistically different from those for the yellowfin tuna, with the exception of heart mass.

bluefin tuna; Davie 1987). The atrial mass was 0.05–0.06% of body mass in both species.

Cardiac dynamics in yellowfin tuna

The individual responses of perfused yellowfin tuna hearts to changes in filling pressure are shown in Fig. 1. Two important points emerge. First, physiological stroke volumes were achieved at subambient filling pressures. Second, stroke volume increased with increased filling pressure in accordance with the Frank–Starling mechanism. Generally, the yellowfin tuna heart was most responsive to filling pressure at stroke volumes that produced subphysiological cardiac output values. We were reluctant to extend this relationship by decreasing cardiac output below 60 mL/(min · kg) because a low cardiac output usually led to irreversible cardiac failure. The largest stroke volume on each Frank–Starling curve was termed maximum stroke volume. Accordingly, the maximum stroke volume for perfused yellowfin tuna hearts was 0.87 ± 0.10 mL/kg body mass (Table 1). The maximum cardiac output (108 ± 4.0 mL/(min · kg body mass); Table 1) was 94% of that measured *in vivo* (115 mL/(min · kg body mass); Bushnell 1988).

Heart rates ranged from 101 to 157 bpm in yellowfin tuna. Beyond an initial decrease in heart rate from the maximum heart rate of 137.6 ± 4.8 bpm to a stable value of 123.3 ± 4.2 bpm (Table 1), heart rate was not significantly affected by normal manipulations in filling pressure and diastolic output pressure. However, excessive increases in diastolic output pressure resulted in arrhythmia. Normal cardiac pumping could be restored by immediately lowering the diastolic output pressure.

The individual responses of perfused yellowfin tuna hearts to increases in diastolic output pressure are shown in Fig. 2. The hearts were capable of homeometric regulation in that

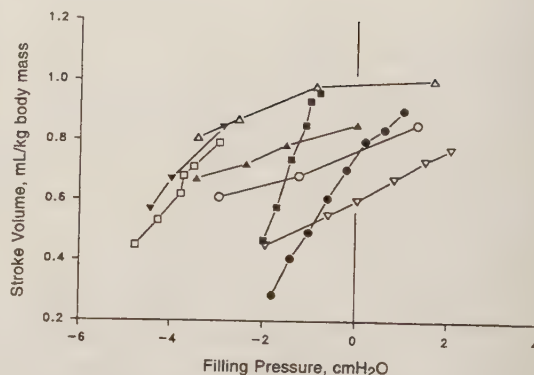


FIG. 1. Individual curves showing responses of cardiac stroke volume to increases in venous filling pressure in perfused yellowfin tuna hearts. There were no further increases in stroke volume beyond the maximum values shown for each curve. It is important to note that the majority of the curves were generated at subambient filling pressures, suggesting a *vis a fronte* filling mechanism for the yellowfin tuna heart.

generally there was little decrement in stroke volume when diastolic output pressures were raised to produce mean output pressures ranging between 130 and 170 cmH₂O (Fig. 2A). The mean maximum output pressure was 145.1 ± 5.8 cmH₂O (Table 1), which exceeds the mean ventral aortic pressure observed *in vivo* by 21% (120 cmH₂O; Bushnell 1988). At the maximum output pressure, cardiac output (97.5 ± 3.5 mL/(min · kg body mass)) was 10% lower than the maximum cardiac output.

Power output increased with output pressure (Fig. 2B). A plateau in power output with increasing output pressure was observed in only one preparation before arrhythmias developed. Therefore, the greatest power output on each curve was termed maximum cardiac power output. Maximum cardiac power output was 7.58 ± 0.44 mW/g ventricular mass or 21.9 ± 1.04 mW/kg body mass (Table 1). Comparisons of cardiac power output relative to body mass are valuable because ventricular mass varies significantly between fish species.

Pulse pressures were unusually large compared with the situation *in vivo*. The average maximum systolic pressure (178 cmH₂O; Table 1) was 33 cmH₂O higher than the mean pressure. This was primarily a result of the high peak flow rate through the output cannula. We minimized cannula resistance by using a tube with the largest bore and shortest length possible. Nonetheless, with peak systolic work being unusually high for a given mean output pressure, maximum power output, which we calculated from the mean output pressure, may underestimate the work performed by the perfused heart.

Cardiac dynamics in skipjack tuna

Although the surgical procedures used for the skipjack tuna and yellowfin tuna were identical, the perfused skipjack tuna heart performed poorly. Typically, hearts could generate a near physiological cardiac output but only at subphysiological diastolic output pressures. Moreover, increasing diastolic output pressure to physiological levels often produced rapid declines in cardiac output and irreversible cardiac failure. The ability of the perfused heart to generate pressure deteriorated

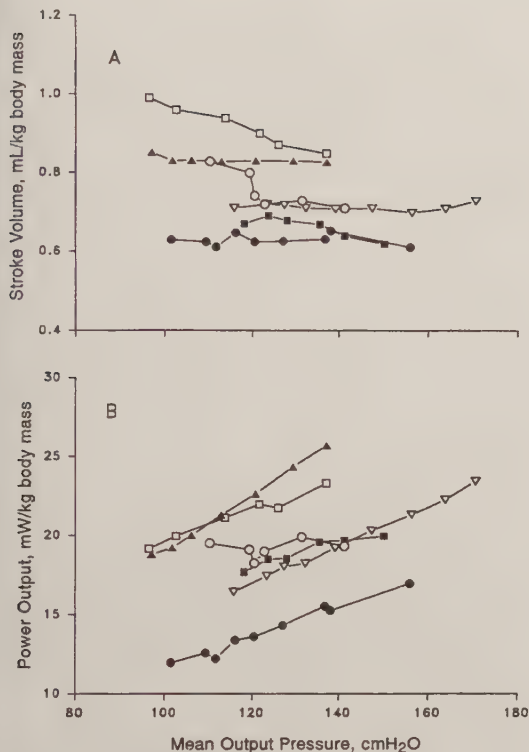


FIG. 2. Individual curves for the response of cardiac stroke volume (A) and power output (B) to increases in diastolic output pressure in perfused yellowfin tuna hearts. Stroke volume was largely independent of output pressure over the range 130–170 cmH₂O. As a result, increases in output pressure produced significant increases in myocardial power output up to the maximum indicated. Increases in output pressure beyond those shown resulted in cardiac arrhythmia. An incomplete range of output pressures was tested on two additional preparations, and these are not included in the figure.

with time. Preparations rarely lasted 30 min. To check whether or not extracellular substrate was a limiting factor, 0.7 mM palmitate in 10% bovine serum albumin, or 5 mM lactate, or both were included in the perfusate in 4 preparations. Addition of these substrates did not improve either the maximum performance or the longevity of the preparation. In an attempt to understand the proximate cause of cardiac failure, lactate levels were measured in the output perfusate. In 5 heart preparations, lactate release into the perfusate ranged from 0.4 to 1.2 $\mu\text{mol}/(\text{min} \cdot \text{g ventricular mass})$, indicating substantial anaerobic metabolism. Lactate release into the perfusate could not be quantitatively related to cardiac work, but the rate of lactate release was comparable to the rate of release in severely hypoxic, working, perfused trout hearts (Arthur *et al.* 1992). The change in P_{O_2} between input and output perfusate samples was never more than 100 Torr (1 Torr = 133.3 Pa). This means that oxygen was not depleted from the perfusate and the diffusion gradient driving oxygen from the lumen into the myocardium was always at least 10 times greater than that normally provided by the venous blood

P_{O_2} (Bushnell 1988). The most likely explanation for high lactate production, despite a very high luminal P_{O_2} , is that oxygen delivery to the myocardium was inadequate.

Attempts to improve oxygen delivery were limited because of the difficulty in cannulating the coronary artery (see below) and a dwindling supply of skipjack tuna. The coronary circulation was perfused with oxygenated saline in 2 preparations by means of an autoperfusion system (connecting a sidearm from the ventral aortic output cannula to the main coronary artery). This procedure did not improve cardiac performance appreciably. Constant pressure perfusion of the coronary circulation with a red blood cell suspension (hematocrit 10%) was attempted in one additional preparation. Red blood cells appeared in the ventral aortic perfusate after less than 1 min, but the coronary flow rate was not measured. Even though there were eventually problems with blood clots, this was the only skipjack tuna heart preparation that performed for longer than 30 min and at output pressures that were physiological.

In view of the above, the data for saline-perfused hearts from skipjack tuna (Table 1) have limited value. In the 10 successful preparations, maximum cardiac output ($84.5 \pm 5.4 \text{ mL}/(\text{min} \cdot \text{kg body mass})$) was 64% of the *in vivo* value ($132 \text{ mL}/(\text{min} \cdot \text{kg body mass})$; Bushnell 1988) when mean output pressure was 74 cmH₂O. The highest individual cardiac output was $112 \text{ mL}/(\text{min} \cdot \text{kg body mass})$. The highest individual stroke volume was $0.86 \text{ mL}/\text{kg body mass}$ and was lower than that *in vivo* ($1.1 \text{ mL}/\text{kg body mass}$; Bushnell 1988). The heart responded to filling pressure, which was often negative, by increasing stroke volume. The range for heart rate in the perfused skipjack heart was 91.1–172.4 bpm. At a mean output pressure of $87.4 \pm 4.0 \text{ cmH}_2\text{O}$, power output increased to a maximum value of $2.55 \pm 0.21 \text{ mW/g ventricular mass}$ or $10.1 \pm 0.88 \text{ mW/kg body mass}$ (Table 1) with only a slight decrease in cardiac output ($82.9 \pm 3.5 \text{ mL}/(\text{min} \cdot \text{kg body mass})$). Higher output pressures significantly decreased cardiac output. All of the maximum values for cardiac variables were significantly lower than those for the yellowfin tuna (Table 1), with the exceptions of the mean (138.5 bpm) and maximum heart rates (154 bpm), which were significantly higher.

Pressure–flow relationships for the skipjack tuna coronary circulation

The pressure–flow relationship for 6 skipjack tuna hearts is summarized in Fig. 3A. The curves for all fish were convex toward the pressure axis at low flow rates, becoming linear at higher flow rates. Vascular resistance decreased exponentially as flow rate (and perfusion pressure) increased. Coronary vascular resistance reached a constant minimum of approximately $24 \text{ cmH}_2\text{O} \cdot \text{min} \cdot \text{g ventricular mass}/\text{mL}$ at a flow rate of $2 \text{ mL}/(\text{min} \cdot \text{g ventricular mass})$ (with perfusion pressure approximately 40 cmH₂O) or higher (Fig. 3B). At high flow rates, 4 of the 6 hearts began to beat spontaneously and eject perfusate from the ventral aorta.

Adrenaline and noradrenaline (α - and β -adrenergic agonists) produced similar concentration-dependent increases in coronary resistance (Fig. 4). Phenylephrine (an α -adrenergic agonist) was a less effective vasoconstrictor. Hearts began to beat more vigorously at high concentrations of adrenaline and noradrenaline, but not with phenylephrine. The amount of perfusate ejected was greater than that being delivered to the heart via the coronary circulation, and we assume that the excess was drawn from the organ bath via the atrium. The highest

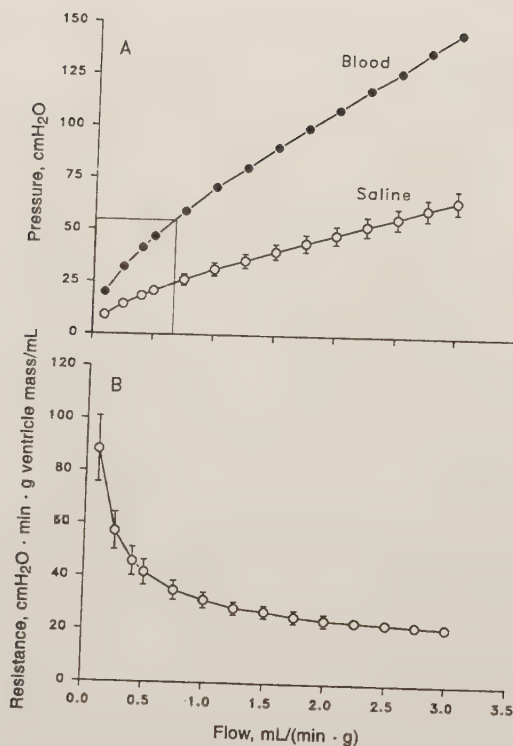


FIG. 3. The coronary perfusion pressure (A) and coronary vascular resistance (B) measured in skipjack tuna hearts perfused with saline at different flow rates. Each point represents a mean value for 6 preparations, and the standard error of the mean is indicated by the vertical bars. In panel A, a pressure-flow relationship is estimated for blood, by adjusting the saline line to account for the difference in the viscosities of tuna blood and the saline perfusate. There are no measurements of kinematic blood viscosity in tuna, and so a value of 2.5×10^{-3} Pa · s was assumed. This value is based on an assessment of known blood viscosities in fish (e.g., Wood 1974; Graham 1985; Graham and Fletcher 1983; Wells and Baldwin 1990; Baldwin and Wells 1990; Wells and Weber 1991). Saline was assumed to have a viscosity of 1×10^{-3} Pa · s at 25°C (Graham 1985). From the curve for blood an *in vivo* coronary blood flow was estimated for a dorsal aortic blood pressure of 55 cmH₂O (Bushnell 1988).

concentration of isoproterenol (a β -adrenergic agonist) made the hearts beat more vigorously and also produced a modest increase in vascular resistance (+5%).

Acetylcholine produced a small increase in vascular resistance in 1 preparation and a small decrease in resistance in another. ADP produced a small decrease in vascular resistance in 1 preparation and no response in another. In the preparation that responded to ADP, vascular resistance was initially slightly elevated (a residual effect from an earlier adrenaline injection) and vascular resistance was reduced only to the normal baseline level. The preparation that did not respond to ADP also did not respond to acetylcholine or adrenaline.

In a preliminary experiment, noradrenaline (10 μ M) and acetylcholine (10 μ M) were injected together in 1 preparation. The resulting contraction was stronger and lasted several

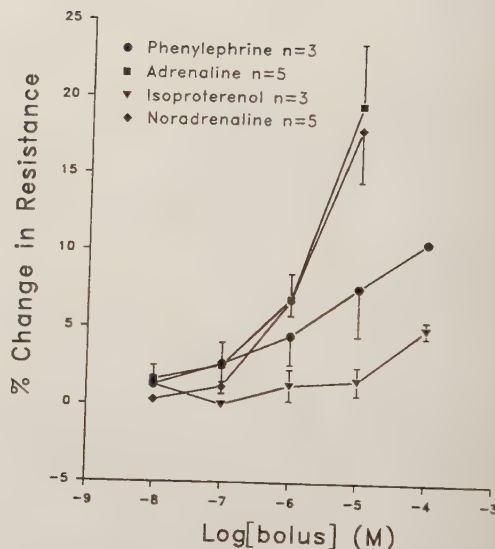


FIG. 4. The vascular reactivity of the coronary circulation in skipjack tuna perfused with oxygenated saline at a constant flow rate (1 mL/(min · g ventricular mass)). Each drug was injected as a bolus (0.1 mL) into the perfusion line. The concentration of the bolus is presented. Responses (percentage change from the baseline resistance) are presented as mean values for 3–5 preparations, and the standard error of the mean is indicated by the vertical bars.

minutes longer than that normally associated with noradrenaline alone. Similarly, when ADP (10 μ M) and noradrenaline (10 μ M) were injected together in 1 preparation, the resulting constriction was more prolonged but was reduced compared with that normally associated with noradrenaline alone.

Discussion

The study of tuna cardiovascular physiology *in vivo* is hampered by the supply, holding, and handling of the fish, and the fact that tunas are normally continuous swimmers. Probably the best set of cardiovascular data are from spinally blocked tunas (Bushnell 1988), even though it is difficult to relate these data to a normal physiological state. Based on our past experience with perfused fish hearts (six fish species, including two active ones), we expected that an *in situ* preparation would provide information regarding maximum cardiac performance in tunas. In view of this expectation, perhaps the most important observation was that saline-perfused preparations of yellowfin and skipjack tuna hearts were unable to match all of the cardiac variables previously measured in live, spinally blocked tunas (Bushnell 1988). The yellowfin tuna heart preparations performed very near, but not above, the *in vivo* cardiac output, whereas the skipjack tuna heart preparations performed below the *in vivo* cardiac output. Intrinsically heart rates were, nevertheless, greater than the *in vivo* values. Interestingly, the maximum *in vivo* power output in rainbow trout is 7.2 mW/g ventricular mass and this can be simulated *in vitro* with aerated saline and no coronary perfusion (Milligan and Farrell 1991). The maximum power output obtained for perfused yellowfin tuna hearts was similarly 7.58 mW/g ventricular mass.

Several observations lead us to conclude that, in the absence of coronary perfusion, the relatively thick ventricle wall of the perfused skipjack tuna heart prevented the supernormal oxygen gradient from providing a sufficient rate of oxygen diffusion from the lumen to support a physiological work output. First, high levels of lactate appeared in the perfusate leaving skipjack tuna hearts. Second, perfused hearts were very sensitive to increases in diastolic output pressure (i.e., an increase in myocardial oxygen demand with no change in luminal oxygen supply). Third, perfused hearts were also very sensitive to reductions in cardiac output (i.e., a decrease in luminal oxygen supply). Fourth, a much higher cardiac performance was possible in yellowfin tuna hearts, which were 38% smaller than the hearts of skipjack tuna. In fact, we found a significant negative correlation between mass specific maximum power output and ventricular mass for skipjack tuna (power output = $15.2 - 1.18(\text{ventricular mass})$; $r = 0.502$, $p < 0.05$).

Thus, even though the relatively larger heart in tunas is advantageous in terms of cardiac performance, the heart appears to be necessarily more dependent on its coronary circulation to overcome increased diffusion distances from the lumen. It seems likely that tuna hearts, particularly those of skipjack tuna, cannot support resting levels of cardiac performance without a coronary circulation. This contrasts with salmonids; they survive after the coronary artery has been ligated (to eliminate the coronary route for myocardial oxygen supply) and then can swim quite well in normoxic and hypoxic water (Farrell and Steffensen 1987; Farrell *et al.* 1990; J. F. Steffensen and A. P. Farrell, unpublished observations).

We made limited attempts to perfuse the coronary circulation and thereby improve oxygen delivery to the *in situ* heart. Coronary cannulation was technically very difficult, and the results obtained were inconclusive. The coronary artery lies next to the thin-walled jugular veins. Thus, it was very difficult to tie the coronary cannula in place without puncturing the veins. Once punctured, leakage of perfusate from the sinus venosus via the jugular veins was substantial. Another technical problem related to the choice of fluid to perfuse the coronary circulation. The suggestion that air- or oxygen-equilibrated salines are adequate for perfusion studies with fish hearts (Perry and Farrell 1988) is clearly not valid for tuna hearts, given the present observations. Perfusion with a red blood cell suspension appears to be a more promising option, given the present observation of improved preparation viability. Even so, the difficulty in obtaining sufficient tunas to provide a pool of blood donors and preventing blood clotting may favour the use of perfluorinated carbon compounds in the future.

The observation that active fishes with higher blood pressures have more compact myocardium has led to the suggestion that the compact layer is more important in pressure development (see reviews by Tota 1983, 1989). Physiological studies also support this idea. Coronary ligation in hypoxic, swimming rainbow trout reduces ventral aortic blood pressure (J. F. Steffensen and A. P. Farrell, unpublished observations). Furthermore, coronary perfusion with red blood cells in hypoxic dogfish and eel hearts improves the ability of the heart to develop pressure (Davie and Farrell 1991a; Davie *et al.* 1992). The present observation of a limited ability to generate high output pressures by perfused tuna hearts is also consistent with the idea of the compact myocardium being more important in pressure development.

Only small increases in cardiac filling pressure are needed

for two- to three-fold increases in stroke volume with perfused hearts from other fishes (sea raven, rainbow trout, ocean pout (*Macrozoarces americanus*), eel (*Anguilla dieffenbachii*), dogfish (*Squalus acanthias*), and kingfish (*Seriola lalandi*) (Farrell 1984; Farrell *et al.* 1985; Farrell *et al.* 1986; Davie and Farrell 1991a; Davie *et al.* 1992; D. Hutchison, C. E. Franklin, and P. S. Davie, unpublished observations). In contrast, perfused yellowfin tuna hearts were less sensitive to filling pressure. There are two potential explanations for this weak response to filling pressure: either the maximum stroke volume observed here is close to the maximum *in vivo* value, or stroke volume was severely limited by insufficient oxygen delivery to the myocardium. We favour the former explanation for a number of reasons. First, stroke volume did not increase beyond the observed maximum level when diastolic output pressure was reduced (i.e., oxygen demand was lower). In fact, perfused yellowfin tuna hearts could maintain stroke volume at output pressures higher than those *in vivo*. Second, when yellowfin tuna and skipjack tuna were exposed to moderate environmental hypoxia (> 80 Torr), stroke volume was unchanged and cardiac output declined in proportion with the bradycardia (Bushnell 1988; Bushnell *et al.* 1990). In contrast, other fish exposed to moderate levels of hypoxia typically developed bradycardia that was accompanied by an increase in stroke volume (Randall 1970; Farrell 1984; Chan 1986; Peyraud-Waitzenegger and Soulier 1989). Therefore, we propose that the maximum anatomical and physiological limit for stroke volume in yellowfin tuna is near the value of 1.3 mL/kg body mass, as determined for spinally blocked yellowfin tuna by means of a dye dilution technique (Bushnell 1988).

If this conclusion proves to be correct, tunas would necessarily alter heart rate to increase cardiac output appreciably, with stroke volume being relatively fixed. This type of cardiac pumping strategy resembles that in mammals rather than that in other teleosts, in which increases in stroke volume are the primary means of increasing cardiac output during exercise (see Farrell 1991). Brill and Bushnell (1991) analyzed the existing cardiovascular data for tunas and suggested that cardiac output would increase approximately twofold to account for the maximum oxygen uptake in skipjack tuna. Since the heart rate in tunas spans a twofold range (see Introduction), there is no need to postulate a major increase in stroke volume.

An interesting pattern may be emerging if the maximum stroke volume in tunas is indeed near 1 mL/kg body mass. Maximum stroke volumes are also near 1 mL/kg body mass in other fishes capable of impressive swimming feats, such as rainbow trout (Graham and Farrell 1989), kingfish (D. Hutchison, C. E. Franklin, and P. S. Davie, unpublished observations), and eel (Davie *et al.* 1992). This stroke volume may represent the upper limit for active teleosts that develop high levels of blood pressure and cardiac output. In contrast, hemoglobin-free icefish, with a high cardiac output and a low blood pressure, have a very high stroke volume (estimated at 4 mL/kg body mass; Hemmingsen *et al.* 1972). Further studies on the interrelationships between chamber size, pressure development, wall thickness, and oxygen delivery to the myocardium would be worthwhile to develop a general hypothesis regarding the maximum cardiac stroke volume in fishes.

Lai *et al.* (1987) observed subambient intrapericardial pressures in albacore (*Thunnus alabunga*) and suggested *vis a fronte* atrial filling. The subambient filling pressure required

to generate near normal stroke volumes in perfused yellowfin tuna hearts is consistent with *vis a fronte* atrial filling. Our most graphic observation in support of *vis a fronte* filling was the aspiration of air into the heart when the hepatic vein was cut. *Vis a fronte* cardiac filling is also found in elasmobranchs (Satchell 1971) and rainbow trout (Farrell *et al.* 1988). Farrell *et al.* (1988) note that the rigid pericardial cavity, which is necessary for *vis a fronte* filling, restricts any increase in the volume of the cardiac chambers, e.g., when stroke volume is increased. Elasmobranchs solve this problem by displacing pericardial fluid into the peritoneal cavity when stroke volume and intrapericardial pressure increase (Shabetai *et al.* 1985). In contrast, tuna may circumvent this particular problem by varying heart rate instead of stroke volume to increase cardiac output.

Myocardial power output has not been calculated previously for tunas. We used the ventral aortic blood pressure and cardiac output reported for spinally blocked yellowfin tuna and skipjack tuna (Bushnell 1988; Brill and Bushnell 1991), and assumed a relative ventricular mass as reported in Table 1 to estimate myocardial power output *in vivo*. In skipjack tuna, power output is 4.7 mW/g ventricular mass (or 18.8 mW/kg body mass), and in yellowfin tuna, power output is 5.6 mW/g ventricular mass (or 16.8 mW/kg body mass). Compared with these *in vivo* values, the maximum myocardial power output in perfused yellowfin tuna hearts (7.58 mW/g ventricular mass; Table 1) could exceed the *in vivo* value by 35%, whereas perfused skipjack tuna hearts produce only 54% of the *in vivo* value. Surprisingly, the *in vivo* power output per gram ventricular mass in spinally blocked tuna is less than the maximum value for rainbow trout (7.2 mW/g ventricular mass, see Farrell *et al.* 1988). To what degree cardiac performance in tunas increases beyond these levels is not clear. We measured levels 35% higher in yellowfin tuna. Brill and Bushnell (1991) suggest that cardiac output could double. If myocardial power output per gram ventricular mass can be twice that in rainbow trout, the biochemical and physiological organization responsible for a difference of this sort are worth investigating.

The truly exceptional performance of the tuna heart becomes apparent when the large ventricle is considered. The yellowfin tuna and skipjack tuna ventricles are over 4 times and almost 6 times larger, respectively, than the rainbow trout ventricle (0.07% of body mass at 15°C; Graham and Farrell 1990). When myocardial power output is expressed per kilogram body mass to account for the species difference in relative heart size, the power outputs for skipjack and yellowfin tunas (18.8 and 16.8 mW/kg body mass, respectively) are nearly 10 times greater than the maximum value for rainbow trout (2.0 mW/kg body mass, Graham and Farrell 1990).

The present study established a pressure-flow relationship for the coronary circulation of skipjack tuna. It is possible to estimate *in vivo* coronary flow from this relationship (Fig. 3A) by adjusting for the difference in viscosities for blood and saline and using a known value for dorsal aortic blood pressure in skipjack tuna (55 cmH₂O; Bushnell 1988; Brill and Bushnell 1991). Since there are no measurements of kinematic blood viscosity in tuna, a value of 2.5×10^{-3} Pa·s was assumed. This value is based on an assessment of known blood viscosities in fish (e.g., Wood 1974; Graham 1985; Graham and Fletcher 1983; Wells and Baldwin 1990; Baldwin and Wells 1990; Wells and Weber 1991). Obviously, the uncertainty regarding the exact blood viscosity in tunas has an

TABLE 2. Predicted coronary flow rates in skipjack tuna and rainbow trout

Coronary flow rate	Skipjack tuna	Rainbow trout ^a	Ratio
mL/(min · g ventricular mass) ^b	0.67	0.38	1.76
mL/(min · g compact tissue) ^c	1.02	0.97	1.03
mL/(min · kg body mass) ^d	2.60	0.27	9.6
Proportion of resting cardiac output ^e	1.9%	1.5%	1.31

^aData taken from Farrell (1987).

^bValue interpolated from Fig. 3A.

^cThe coronary circulation perfuses only the compact myocardium in rainbow trout. The exact perfusion pattern in tuna is unknown. The proportion of compact myocardium is greater in the skipjack tuna ventricle (65%) than in the rainbow trout ventricle (39%). The value was calculated as (mL/(min · g ventricular mass))/0.65.

^dThe skipjack tuna ventricle (0.4% body mass) is relatively larger than the rainbow trout ventricle (0.07% body mass). The value was calculated as (mL/(min · g ventricular mass)) × (% relative ventricular mass) × 10.

^eCardiac output in spinally blocked skipjack tuna (132 mL/(min · kg body mass)) is higher than in resting rainbow trout (17 mL/(min · kg body mass)). The value was calculated as $100 \times (\text{coronary flow, in mL/(min · kg body mass)})/(\text{cardiac output, in mL/(min · kg body mass)})$.

important impact on the flow estimate. If tuna blood viscosity is 2.0×10^{-3} Pa·s, coronary blood flow *in vivo* would be 20% lower than that presented. Conversely, if tuna blood viscosity is 3.0×10^{-3} Pa·s, coronary blood flow *in vivo* would be 20% greater than that presented.

The estimate of coronary blood flow for the above conditions is 0.67 mL/(min · g ventricular mass) (Fig. 3A; Table 2). From a physiological standpoint, this estimate probably should be regarded as a maximum flow rate for a given blood pressure because there was limited vascular tone in the coronary circulation (see below), and extravascular compression of coronary circulation was negligible (the afterload was minimal and the heart was not beating except at high flow rates). Extravascular compression, as a result of increasing heart rate, increased vascular resistance by 20–25% in the perfused rainbow trout hearts (Farrell 1987) and by 6–14% in the mammalian hearts (Feigl 1983).

The estimated coronary blood flow of 0.67 mL/(min · g ventricular mass) for skipjack tuna is 76% higher than the estimated value for rainbow trout obtained with an identical approach (Farrell 1987). The difference reflects a somewhat lower minimum vascular resistance in skipjack tuna (24 cmH₂O · min · g ventricular mass/mL; Fig. 3B) compared with rainbow trout (36 cmH₂O · min · g ventricular mass/mL; Farrell 1987) and a higher dorsal aortic blood pressure in skipjack tuna. The compact myocardium is proportionately larger in skipjack tuna. When coronary flow rate is expressed per unit mass of compact myocardium, the coronary flow rates are remarkably similar for the two species (Table 2). However, total coronary flow for skipjack tuna (expressed per kilogram body mass) is 9.6 times greater than that for rainbow trout (Table 2) because the tuna ventricle is approximately 6 times larger than that of the rainbow trout heart.

Cardiac output is also approximately 6 times greater in skipjack tuna than in rainbow trout. Therefore, the relative proportion of cardiac output going to the skipjack tuna heart is 1.9% (Table 2). Based on estimates with microspheres, coronary flow was 0.65% of cardiac output in the sucker (*Catostomus commersoni*) and 0.56% of cardiac output in the burbot (*Lota lota*) (Cameron 1975). Based on pressure-flow curves and similar assumptions to those used here, coronary flow in rainbow trout was estimated at 1.5% (Farrell 1987). Thus, even

though the proportion of cardiac output going to the coronary circulation is the highest so far reported for fish, the value is only 31% higher than for rainbow trout. Given the uncertainty regarding blood viscosity in tuna, the most important point to emerge from the above theoretical analysis is that the very high body mass specific cardiac output in skipjack tuna appears to be matched by a very high body mass specific coronary blood flow rate.

Based on the present study some tentative conclusions about the control of coronary flow in skipjack tuna can be made. From Fig. 3A the dorsal aortic blood pressures needed to double (85 cmH₂O) or triple (110 cmH₂O) coronary blood flow are high relative to *in vivo* values. While blood pressure is likely a major determinant of the coronary blood flow rate, a vasodilatory reserve could also contribute to hyperemia, as is the case in the mammalian heart (Feigl 1983). Adrenaline and noradrenaline constrict the coronary circulation of skipjack tuna, rainbow trout, and blue marlin (*Makaria nigricans*) (Davie and Daxboeck 1984; Farrell 1987). Thus, an α -adrenergic tonic vasoconstriction could be involved in the coronary vasodilatory reserve in fish. Adrenergic coronary vasoconstriction in rainbow trout is temperature dependent, being much less pronounced at 15 than at 5°C (Farrell 1987). Correspondingly, the adrenergic vasoconstrictions in skipjack tuna at 25°C were modest relative to those in rainbow trout. Synergistic interactions with catecholamines are worth further study. Our preliminary observations indicate that either ADP and noradrenaline, or acetylcholine and noradrenaline, prolong and alter the intensity of adrenergic vasoconstrictions. Synergistic actions of noradrenaline and adenosine have been reported previously for atrial and ventricular strips from the flounder (*Platichthys flesus*) (Lennard and Huddart 1990), and for mammalian cardiac tissue (Wilson and Broadley 1989). Pharmacological agents expected to significantly dilate the coronary circulation (isoproterenol and ADP) did not do so, probably because there was no vascular tone against which dilatation could be measured. The modest increase in vascular resistance with isoproterenol was a result of either extravascular compression as the heart began to contract, or a nonspecific action of isoproterenol which normally dilates coronary vessels in other fish species (Davie and Daxboeck 1984; Farrell and Graham 1986; Small *et al.* 1990; Davie and Farrell 1991b; Farrell and Davie 1991). While *in vitro* perfusion studies will continue to be useful in identifying potential vasoactive mechanisms, measurements of coronary blood flow *in vivo* are needed to fully understand coronary circulatory control in fish.

In summary, tunas are very active fishes and need high rates of oxygen delivery to their tissues. High levels of blood flow, ventral aortic blood pressure, and blood oxygen carrying capacity are needed to sustain this activity. High flow and pressure are generated by a large heart which has a relative mass comparable with that of mammalian hearts. Because of the ventricle's high myocardial oxygen demand and large diffusion distance from the lumen, venous blood is unlikely to ever satisfy the normal myocardial oxygen demand. Thus, tunas differ from other fishes examined so far in that venous blood apparently cannot support resting cardiac performance; a coronary circulation is essential. Furthermore, the very high body mass specific cardiac output in skipjack tuna appears to be matched by a very high body mass specific coronary blood flow rate. The outer compact myocardium and its coronary oxygen supply appear to be more important for pressure

development by the heart than for flow output. Consequently, if dorsal aortic blood pressure is reduced, either through impaired cardiac performance or elevated gill resistance, then coronary flow will likely decrease. The effects of interruption of coronary flow in tunas are probably similar to those in mammals, where ischemia depresses cardiac performance which, in turn, further impairs coronary flow and infarction ensues.

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Physical and biological effects of Los Niños in the eastern tropical Pacific, 1986–1989

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Abstract—The eastern tropical Pacific Ocean was surveyed in August–November 1986, 1987, 1988 and 1989 as part of a long-term program to monitor dolphin stocks. Temperature, salinity, chlorophyll and nutrients were monitored to help interpret variability in dolphin stock estimates. The four surveys reveal major environmental changes during the moderate 1987 El Niño and the cold La Niña episode that followed in 1988. During the “onset” phase of El Niño in fall 1986, surface temperatures were up to 1.5°C above normal in equatorial water, but near normal in tropical water north of the equator. The equatorial thermocline ridge was deepened by 10–30 m. During the “mature” phase of El Niño in fall 1987, surface temperatures anomalies were up to +2.5°C in equatorial water and about +1°C in tropical water. Thermocline topography was anomalously flat. Surface chlorophyll and nutrient concentrations declined by 11–48% compared to 1986, with the greatest declines occurring in coastal and equatorial upwelling systems and along the countercurrent thermocline ridge. During La Niña 1988, equatorial surface temperatures were up to 2.5°C below normal and the equatorial thermocline ridge was 10–50 m more shallow than normal. Chlorophyll and nitrate concentrations increased by 58–65% compared to 1987. In 1989, surface temperature was within $\pm 1^\circ\text{C}$ of normal throughout the study area and chlorophyll concentrations were similar to those observed in 1986. Changes in nutrient availability and biological productivity during the El Niño/La Niña cycle were caused by variations in both the rate of wind-driven upwelling and in the nutrient content of subsurface water entrained by upwelling.

INTRODUCTION

THE eastern tropical Pacific Ocean (ETP) contains some of the most productive waters of the world oceans (CHAVEZ and BARBER, 1987) and supports important clupeoid and tuna fisheries. Yet, this region has been surveyed on a large scale only during EASTROPAC in 1967–1968 (BLACKBURN *et al.*, 1970). The ETP is also a region of significant interannual variability associated with the El Niño–Southern Oscillation (ENSO), an internally-driven cycle within the coupled ocean–atmosphere system of the tropical Pacific (ENFIELD, 1989). Since ENSO variability has global atmospheric, oceanic and biological ramifications,

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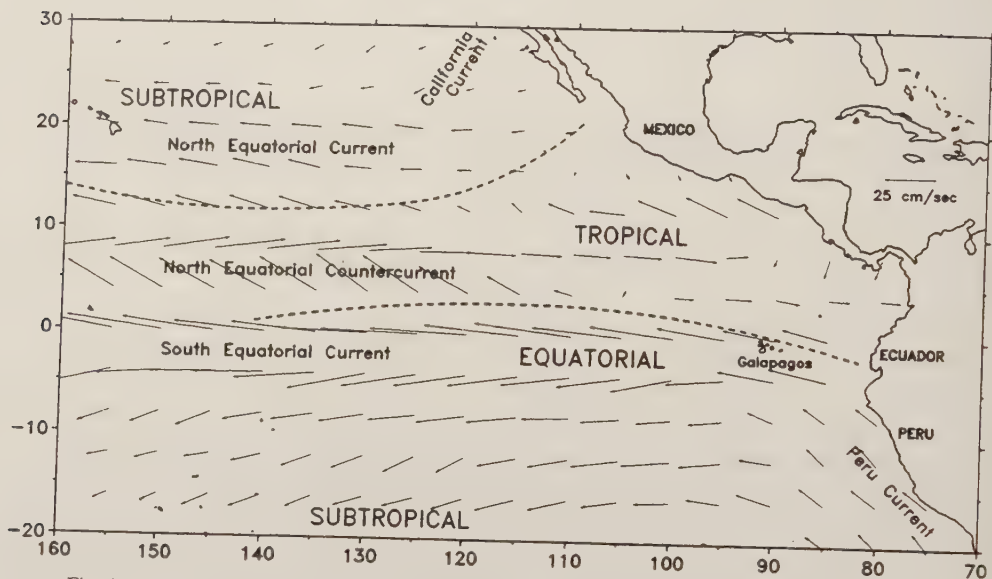


Fig. 1. Eastern tropical Pacific surface water masses (WYRTKI, 1967, 1968) and surface currents (from September–November ship drift data, FIEDLER, in press).

systematic studies of this region are important in order to develop a predictive understanding of the variability. NOAA- and NSF-sponsored studies of the ETP in the last decade (EPOCS, TOGA, TROPIC HEAT) have been restricted to meteorological and physical oceanographic variables (HAYES *et al.*, 1986), with some minor exceptions (e.g. CHAVEZ and BARBER, 1987).

The ETP is the site of a yellowfin tuna purse seine fishery that interacts with large dolphin populations (PERRIN, 1969). In 1986, the National Marine Fisheries Service, Southwest Fisheries Science Center, began a 5-year survey program to monitor trends in dolphin stock abundance in the ETP. Physical and biological data have been collected during dolphin census operations to help interpret variations in stock estimates and to investigate basic questions about dolphin distribution and ecology. We report here the chlorophyll, nutrient and temperature results from the first 4 years of this monitoring program. We discuss spatial patterns of the biological variables, which have never before been measured on this scale in the ETP, and interannual variability associated with El Niño 1986–1987 and La Niña 1988.

BACKGROUND

There are three principal surface water masses in the ETP: tropical surface water, subtropical surface water, and equatorial surface water (Fig. 1). Each of these water masses has characteristic properties determined by climate regimes at local or remote points of origin. Tropical surface water is found in the center of the ETP, along 10°N. It is the warmest, lowest-salinity, and least seasonally variable water in the ETP. Salinity is low

because rainfall exceeds evaporation beneath the cloudy and rainy Intertropical Convergence Zone (ITCZ). Tropical surface water is warmest in May–August, although seasonal variation of temperature is low ($\leq 1^{\circ}\text{C}$, HOREL, 1982; FIEDLER, in press). This suggests that seasonal temperature changes are caused by variations in local heating.

Cool, high-salinity subtropical surface water is found toward the poleward edges of the ETP, in the subtropical gyres of the North and South Pacific. In these regions, seasonal variability is higher than in the tropics: SSTs are generally warmest during the summer seasons of the respective hemispheres (HOREL, 1982; FIEDLER, 1991). Evaporation greatly exceeds rainfall, and surface salinity is over 36 psu in the center of the subtropical gyres.

Equatorial surface water is found between the tropical and southern subtropical surface water masses. It appears as the tongue of cool, moderately saline water extending westward along the equator from the Peruvian coast (Fig. 2). In general, equatorial surface water is coldest during northern summer or autumn, when the southeast trade winds are strongest. Seasonal temperature variations are larger near the coast, and the phase of the variations propagates westward from the coast (HOREL, 1982). Thus, the coldest SSTs relative to the annual mean occur in August–September near the coast while at 140°W , for example, the coldest SSTs occur in November.

Conflicting theories suggest that the average state of the cold tongue is maintained either by equatorial upwelling and advection of cold water from the Peru Current by the South Equatorial Current (WYRTKI, 1981) or by the eastward advection of cold water by the Equatorial Undercurrent as it rises to the surface near 95°W (BRYDEN and BRADY, 1985). Whichever mechanism may be correct for the average state, advection of water by the SEC may play an important role in variations of sea surface temperature in the cold tongue (cf. LEETMAA, 1983).

In addition to the three oceanic surface water masses, the cool, low-salinity waters of the Peru and California Currents are also found in the ETP. Peru Current water is contiguous with equatorial surface water. Along the Central American coast, small and ephemeral water masses containing cool, recently upwelled water may be present.

The general features of the surface current system (Fig. 1) can be deduced from the average thermocline topography (Fig. 2). The 20°C isotherm is found in the middle of the thermocline and its depth is used to represent thermocline depth in the tropical Pacific (DONGUY and MEYERS, 1987). The depth of the thermocline indicates the thickness of the surface mixed layer within which wind-driven surface currents flow. The westward transport of surface water by the trade winds results in a downward slope of the thermocline, and upward slope of the sea surface, across the tropical Pacific from east to west. Thermocline topography also has a series of zonal ridges and troughs. We use the traditional names of ridges and troughs in sea-level or dynamic height (WYRTKI, 1974) to label the corresponding subsurface troughs and ridges in the thermocline topography.

In accordance with simple geostrophic theory, the spatial variations of the depth of the thermocline reflect the directional tendencies of the largely zonal, near-surface currents of the ETP. In the northern hemisphere the thermocline will be deeper to the right of a current as the observer looks downstream, while in the southern hemisphere the opposite is true. Thus, the broadest current in the ETP, the South Equatorial Current (SEC), flows westward through the region, extending in the cross-stream direction from the southern edge of the ETP across the equator to almost 5°N . North of the countercurrent thermocline ridge at 10°N , where the thermocline slopes downward to the north, the North Equatorial Current (NEC) also flows westward. Along the eastern boundary, the

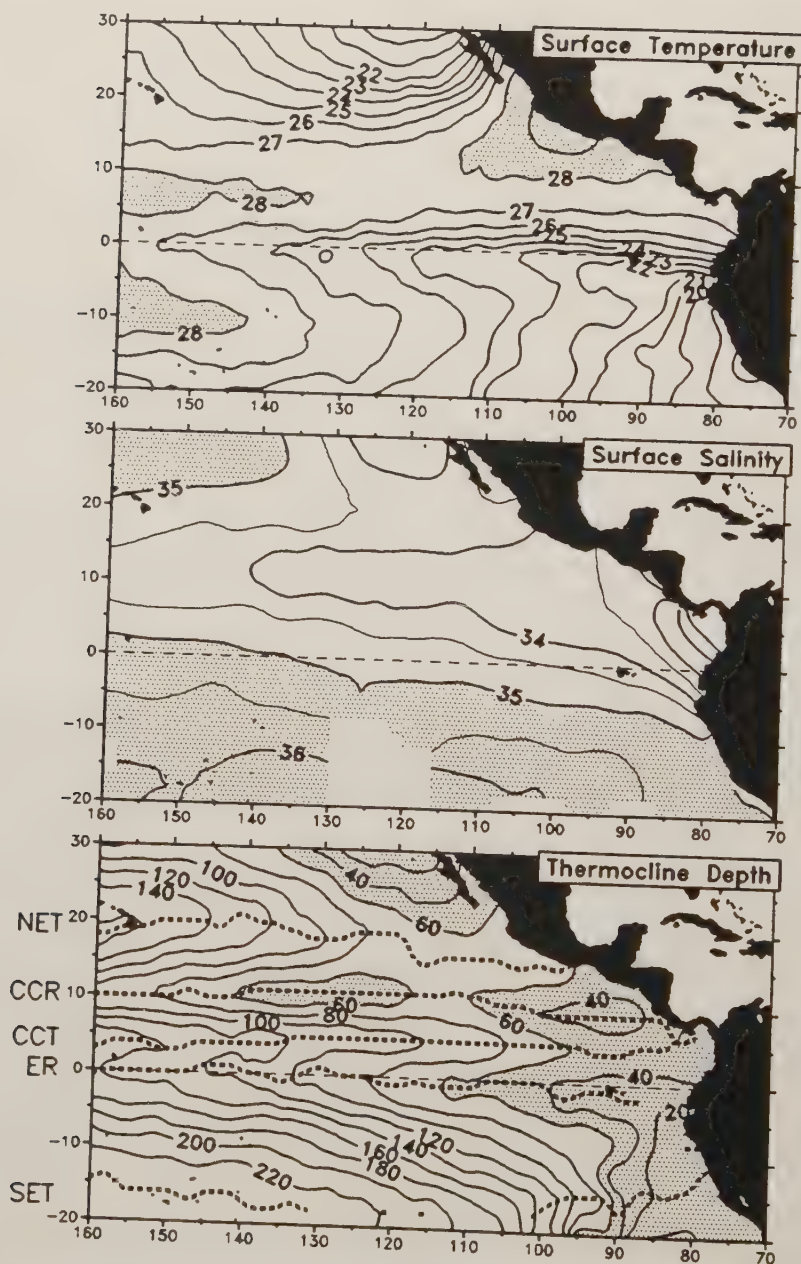


Fig. 2. August–November climatological fields (FIEDLER, in press). (Top) Surface temperature ($^{\circ}\text{C}$), 1928–1988, $n = 70,700$. (Middle) Surface salinity (psu), 1922–1988, $n = 8129$. (Bottom) 20°C isotherm (thermocline) depth (m), 1943–1988, $n = 60,014$. NET = north equatorial trough; CCR = countercurrent ridge; CCT = countercurrent trough; ER = equatorial ridge; and SET = south equatorial trough.

thermocline slopes upward toward the coasts of Peru and Baja California, reflecting the equatorward flow of the Peru and California Currents. These coastal systems feed into the eastern "upstream" ends of the NEC and SEC.

The westward, wind-driven transport of surface water in the tropical Pacific results in a downward slope of the sea surface of about half a meter from west to east. Westward wind stress exceeds the eastward pressure gradient force except in the doldrums, between the northeast and southeast trades. The North Equatorial Countercurrent (NECC) flows eastward between the NEC and SEC, on the southern flank of the countercurrent thermocline ridge. The NECC shows considerable seasonal variation, being strongest during November–December when the slope of the thermocline ridge is steepest (KESSLER and TAFT, 1987). These variations can be largely explained by local Ekman dynamics. The NECC lies in the Intertropical Convergence Zone (ITCZ) where the northeast and southeast tradewinds converge (the doldrums). Wind-stress curl is positive (cyclonic) over the countercurrent thermocline ridge at 10°N, causing Ekman upwelling. Wind-stress curl over the countercurrent thermocline trough at 5°N is negative (anticyclonic), causing Ekman downwelling. As the ITCZ migrates from its northern extreme in fall to its southern extreme in spring, the gradients in wind-stress curl and Ekman pumping velocity weaken, thermocline and sea surface slopes flatten, and flow of the NECC diminishes (FIEDLER, 1991). The phase and amplitude of the variations in the curl are sufficient to account for the variations in the depth of the thermocline ridge and the strength of the NECC (MEYERS, 1979; KESSLER and TAFT, 1987).

Upwelling occurs wherever horizontal divergence of surface waters causes subsurface water to ascend to conserve mass. Both coastal upwelling along eastern boundaries and equatorial upwelling occur in the ETP. Equatorial upwelling is the result of a geostrophic divergence of the wind-driven SEC. The westward component of the southeast trade winds causes poleward Ekman transport of surface water on either side of the equator. The effects of upwelling are evident in the equatorial thermocline ridge and in the anomalously cool temperature of equatorial surface water. SVERDRUP *et al.* (1942) presented evidence of surface divergence and upwelling at two sites in the equatorial current system: along the equator and between the NECC and NEC at 10°N. The countercurrent thermocline ridge is evidence of upwelling, although generally warm temperatures and low nutrient concentrations suggest that the effects of upwelling do not reach the surface (CROMWELL, 1953). Offshore transport of surface waters and coastal upwelling are driven by equatorward longshore winds along the coasts of Baja California and Peru, and by topographically-induced offshore winds at several points along the coast of Central America (Gulfs of Tehuantepec, Papagayo and Panama).

Equatorial water and coastal water (especially in the Peru Current System off Ecuador and Peru) in the ETP normally have a very high biological productivity (CHAVEZ and BARBER, 1987; BARBER and KOGELSCHATZ, 1990). Physical studies on both the coastal and equatorial regimes have shown that upwelled water is entrained usually from 40 to 80 m depth and always less than 100 m (SMITH, 1982; HALPERN and FREITAG, 1987). The thermocline is shallow in these regions, so that vertical advection and mixing bring cold, nutrient-rich water from below the thermocline (nutricline) into the surface layer. This nutrient input maintains optimal (saturating) concentrations of new nitrogen at the surface and results in high levels of new production (CHAVEZ and BARBER, 1987). Depression of the thermocline, as during El Niño, reduces the input of new nitrogen into the surface layer and limits productivity.

Interannual variability in the tropical Pacific Ocean is dominated by the El Niño–Southern Oscillation (ENSO). ENSO is an irregular cycle of variations in atmospheric pressure gradients, surface winds, sea surface temperature, thermocline depth, and biological productivity (CANE, 1983; GRAHAM and WHITE, 1988; ENFIELD, 1989). The response of the ETP to interannual wind variations caused by the Southern Oscillation (surface pressure difference between the Indonesian low pressure center at Darwin, Australia and South Pacific high pressure center at Tahiti) is similar to the response to seasonal variations, although the magnitude of the interannual response is much greater (PHILANDER, 1989). RASMUSSEN and CARPENTER (1982) formulated a composite ENSO event from six events between 1949 and 1976. Relevant characteristics of each phase of the composite ENSO are listed in Table 1.

The interannual variability associated with the ENSO phenomenon since 1975 is shown by the variation of three indices: the Southern Oscillation Index (SOI), based on the sea-level pressure difference between Darwin and Tahiti; the NINO-3 (eastern equatorial Pacific) SST Anomaly; and the Southeast Trade Wind Anomaly (Fig. 3). The variability of these indices during 1986–1989 was extreme, ranging as widely as during the great 1982–1983 ENSO event. By these indices, the 1987 El Niño was beginning in mid-1986, when the Indonesian low was weakening (SOI decreasing) and SST in the eastern equatorial Pacific was becoming anomalously warm. At the same time, an operational model analysis of the tropical Pacific showed that the thermocline was deepening along the equator east of

Table 1. *Tropical Pacific surface temperature, pressure and trade winds in the Rasmusson–Carpenter composite El Niño–Southern Oscillation event (RASMUSSEN and CARPENTER, 1982)*

Antecedent Phase
(a) Negative SST anomalies along Peru–Ecuador coast.
(b) South Pacific high pressure center weakening.
(c) Strong trade winds in the western Pacific.
Onset Phase (September of pre-El Niño year)
(a) SST near normal and rising along Peru–Ecuador coast. Positive SST anomalies in the central Pacific.
(b) South Pacific high reaches a minimum.
(c) Weak trade winds in the western and south Pacific.
Peak Phase (April of El Niño year)
(a) Positive SST anomalies in the eastern and central Pacific are spreading laterally and merging.
(b) Indonesian low approaching a maximum and Southern Oscillation Index approaching a maximum negative anomaly.
(c) Weak or reversed trade winds in the central Pacific.
Transition Phase (September of El Niño year)
(a) Large positive SST anomalies cover entire eastern and central equatorial Pacific, but are decreasing at Peru–Ecuador coast.
(b) South Pacific high is strengthening and SOI becoming less negative.
(c) Weak or reversed trade winds in central and western Pacific.
Mature Phase (January of post-El Niño year)
(a) Positive SST anomalies persist in eastern and central equatorial Pacific. Peru–Ecuador SSTs near normal.
(b) South Pacific high is normal and Indonesian low returning to normal.
(c) Strong trade winds in eastern equatorial Pacific.

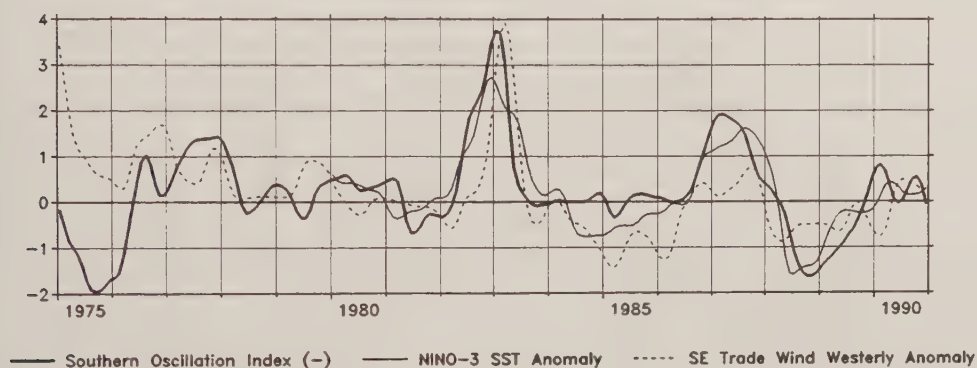


Fig. 3. Smoothed (4253H) monthly time series of (1) Southern Oscillation Index (—), the difference between standardized sea level pressure anomalies at Darwin and Tahiti (Darwin-Tahiti), (2) NINO-3 SST Anomaly, the mean sea surface temperature anomaly ($^{\circ}\text{C}$) in the area 5°N – 5°S and 150°W – 90°W , and (3) Southeast Trade Wind Westerly Anomaly, the standardized 850 mb westerly wind anomaly in the area 5°N – 5°S and 135°W – 120°W . Note that the conventional signs of indices (1) and (3) are reversed, so that positive values of all indices indicate El Niño conditions. Monthly means from Climate Diagnostic Bulletin, NOAA/NWS/NMC/Climate Analysis Center.

150°W (KOUSKY and LEETMAA, 1989). The El Niño “peaked” during the fall of 1987. By late 1987 and early 1988 the indices had rapidly reversed sign and oceanic conditions were shifting to a cold phase, sometimes referred to as La Niña (PHILANDER, 1985). LANDER (1989) concluded that the 1986–1987 ENSO event was 3 months ahead of the Rasmusson-Carpenter composite, although this phase shift was within the range of variability of the six events included in the composite. McPHADEN and HAYES (1990) pointed out that the 1986–1987 ENSO differed from the composite in that warm SST anomalies developed west of 140°W prior to South American coastal warming and that these warm anomalies persisted for 18 months, compared to 12 months in the composite.

Although ENSO events are not all alike, the composite ENSO of RASMUSSEN and CARPENTER (1982) will be a useful point of reference in the discussion that follows. The seasonal cycle of variations in the ETP already discussed above will be second point of reference. Our observations are unique in the repeated intensive spatial coverage of a large oceanic region during a period of major environmental variability.

MATERIALS AND METHODS

NOAA Ships *McArthur* and *David Starr Jordan* surveyed a 14 million km^2 area each year from August to November, 1986–1989. Surface temperature, salinity and *in vivo* fluorescence data are collected continuously while the ships are underway (FIEDLER *et al.*, 1990). Four to six XBTs are deployed daily. CTD data and chlorophyll and nutrient samples are collected at one or two hydrographic stations per day (Table 2). We report here the XBT and hydrographic sample results.

In 1986, Niskin bottles were tripped at 20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 500 and 1000 m. In 1987–1989, bottles were tripped at 20, 40, 60, 80, 100, 125, 150, 250, 350, 500 and 1000 m. Surface water samples were collected from the ships’ seawater systems.

Table 2. Numbers of XBT and CTD casts completed, and nutrient and chlorophyll samples processed for this study

Year	XBT	CTD	Chlorophyll	Nutrient
1986	1678	344	4236	2010
1987	1176	280	2128	1577
1988	821	352	3613	1643
1989	743	352	3552	—
Total	4418	1328	13,529	5230

Chlorophyll and phaeopigments (down to 160 m) were determined by the fluorometric technique using Turner 111 fluorometers calibrated before and/or after each cruise with commercial chlorophyll *a* (Sigma*). Samples (275 ml) were filtered onto 25 mm Whatman GF/F or Gelman A/E glass-fiber filters and extracted for 24–36 h. A saturated magnesium carbonate solution filtered through the Gelman filters before filtering the sample improved retention of small cells (CHAVEZ and BARBER, 1987). Euphotic zone depth was calculated from total pigment profiles according to MOREL (1988).

Water samples for nutrient analysis (down to 500 m) were frozen immediately and returned to Duke University (1986) or Monterey Bay Aquarium Research Institute (MBARI, 1987–1988). Nitrate, nitrite, phosphate and silicate concentrations were determined on a Technicon (Duke) or Alpkem (MBARI) autoanalyzer. Nutrient samples from 1989 have not yet been analysed.

Data were objectively gridded in a 1° latitude–longitude grid using $1/d^2$ weighting ($0.1 \leq d \leq 4$ degrees). Grids were lightly smoothed before contouring (Laplacian smoothing, YOUNG and VAN WOERT, 1987). We statistically analysed the means of data in 2° squares to remove effects of spatial bias of the sampling design, which puts more effort in areas of greater dolphin abundance, and of changes in the distribution of effort between surveys. Interannual changes of chlorophyll and nutrient concentrations were determined by calculating ratios or differences of the 2° means. Contoured interannual ratio or difference maps were used to assess the spatial variability of interannual changes, but are not presented here.

RESULTS

Surface temperature and thermocline depth

In August–November 1986, we observed near-normal surface temperatures (anomalies of 0 to +1°C) and thermocline depths (anomalies of 0 to +20 m) over most of the ETP (Figs 4 and 5). However, along the equator west of 100°W and off the coast of Peru, the thermocline was depressed by 20–30 m and surface temperatures were >1°C above normal. SST anomalies also exceeded +1°C near the Galapagos. In tropical surface water north of the equator, surface temperatures were within about 0.5°C of normal and the depth of the countercurrent thermocline ridge was within 10 m of normal.

In August–November 1987, SST anomalies were +1°C or greater throughout most of the study area south of 10°N and were as large as +2 to +3°C along the equator (Fig. 4).

*Reference to trade name does not imply endorsement by NMFS.

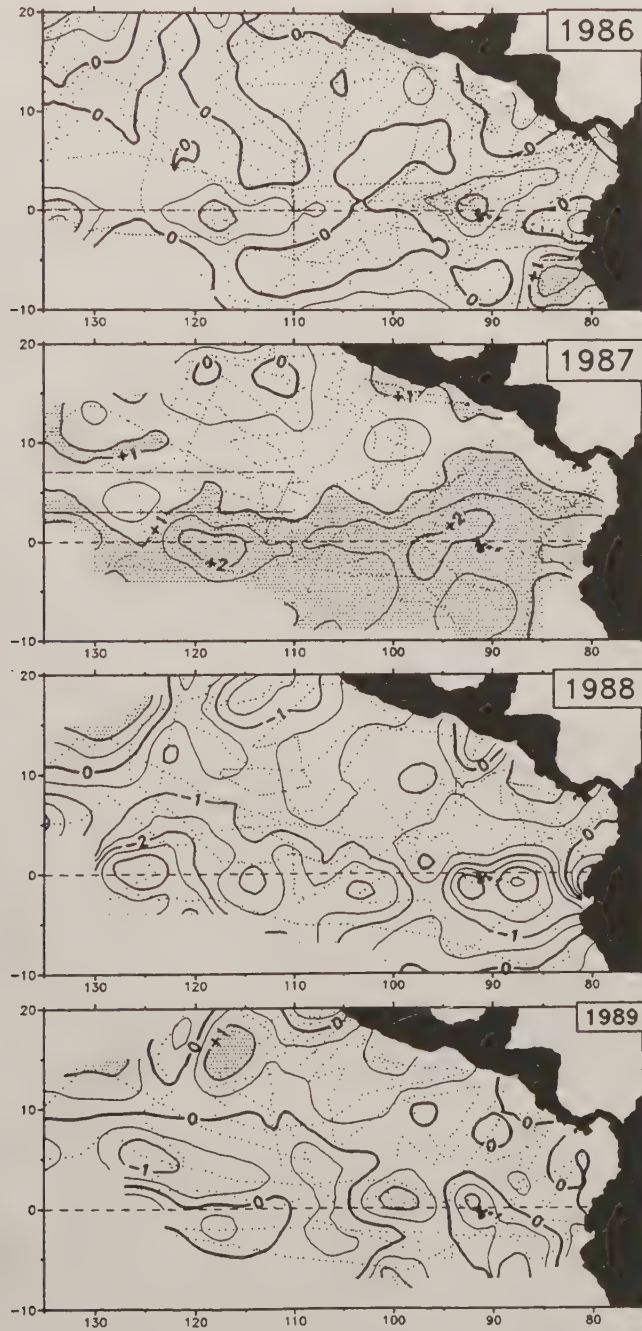


Fig. 4. Surface temperature anomalies ($^{\circ}\text{C}$) from XBTs deployed on MOPS and EPOCS cruises, and by ships of opportunity, August–November 1986, 1987, 1988 and 1989.

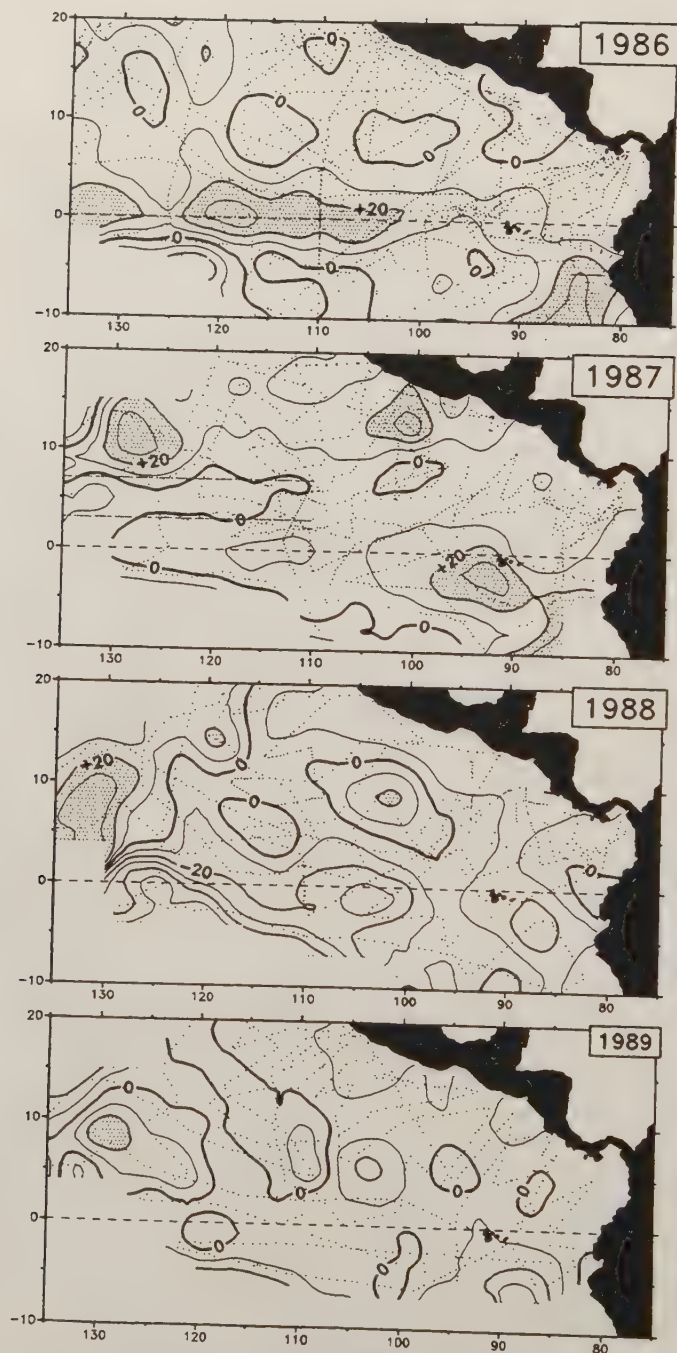


Fig. 5. Thermocline (20°C isotherm) depth anomalies (m) from XBTs, August–November 1986, 1987, 1988 and 1989.

The coldest SSTs in the equatorial cold tongue were only about 23°C, compared to normal SSTs of 21°C or less. The warm band of tropical surface water was warmer than 28°C across the entire study area (not shown). Thermocline depth anomalies appeared in tropical water north of the equator and thermocline topography was generally flatter than normal (Fig. 5). The basin-wide zonal slope was reduced by deepening in the extreme eastern tropical Pacific. Oceanic ridges and troughs were deepened and shoaled, respectively. Thermocline depth on the equator west of 110°W was closer to normal in 1987 than in 1986, although the equatorial thermocline ridge was depressed by 30 m south of the Galapagos.

By August–November 1988, surface temperatures were below normal over almost all of the study area (Fig. 4). The equatorial cold tongue was 0.5–2.5°C colder than normal and 2–4°C colder than in 1987. The 20°C isotherm had broken the surface as far west at 90°W, south of the Galapagos Islands; the coldest SSTs were less than 19°C (not shown). The warm, band of tropical surface water north of the equator had cooled by 1–2°C since 1987, but was not more than 1°C below normal. The equatorial thermocline ridge had shoaled to a depth of 20–40 m less than normal especially west of 100°W. The countercurrent ridge and trough were again well-developed, although the thermocline ridge remained anomalously deep west of 135°W and at the 100–110°W saddle (low point in the ridge, Fig. 2). The deep anomalies in the northwest corner of the study area and shallow (–10 m) anomalies along the Central American coast resulted in an unusually steep zonal thermocline slope.

In August–November 1989, we observed SST anomalies between –0.5 and +1.0°C and thermocline depths within ± 10 m of normal over most of the study area. This year (1989) was the most normal (average) year in our 4-year time series.

Nutrients and chlorophyll

Although El Niño was beginning to affect surface temperature and thermocline structure in the central equatorial Pacific during August–November 1986, we will consider our nutrient and chlorophyll results from both 1986 and 1989 to represent “normal” conditions in the ETP. We present maps of nitrate concentration only (Figs 6 and 7), because phosphate and silicate were strongly correlated with nitrate (Table 3). In addition, regressions of phosphate and silicate on nitrate gave significant positive intercepts (all $P < 0.001$). This means that nitrate was depleted before phosphate or silicate and was more likely to limit productivity. Nitrate concentrations of $< 4 \mu\text{g-at l}^{-1}$ will be considered growth-limiting. At higher concentrations, nitrate uptake by oceanic phytoplankton is saturated (BARBER and KOGELSCHATZ, 1990).

In August–November 1986, surface nitrate concentrations were highest in equatorial water (south of 4°N) and in the region of the Costa Rica Dome (10°N, 90°W, Fig. 6).

Table 3. Regression analysis of phosphate (P) and silicate (S) on nitrate (N) surface and mean euphotic zone concentrations ($\mu\text{g-at l}^{-1}$)

Phosphate		
Surface:	$P = 0.06N + 0.32$	$r = 0.82$
Euphotic zone:	$P = 0.06N + 0.29$	$r = 0.94$
Silicate		
Surface:	$S = 0.39N + 1.84$	$r = 0.77$
Euphotic zone:	$S = 0.50N + 1.80$	$r = 0.88$

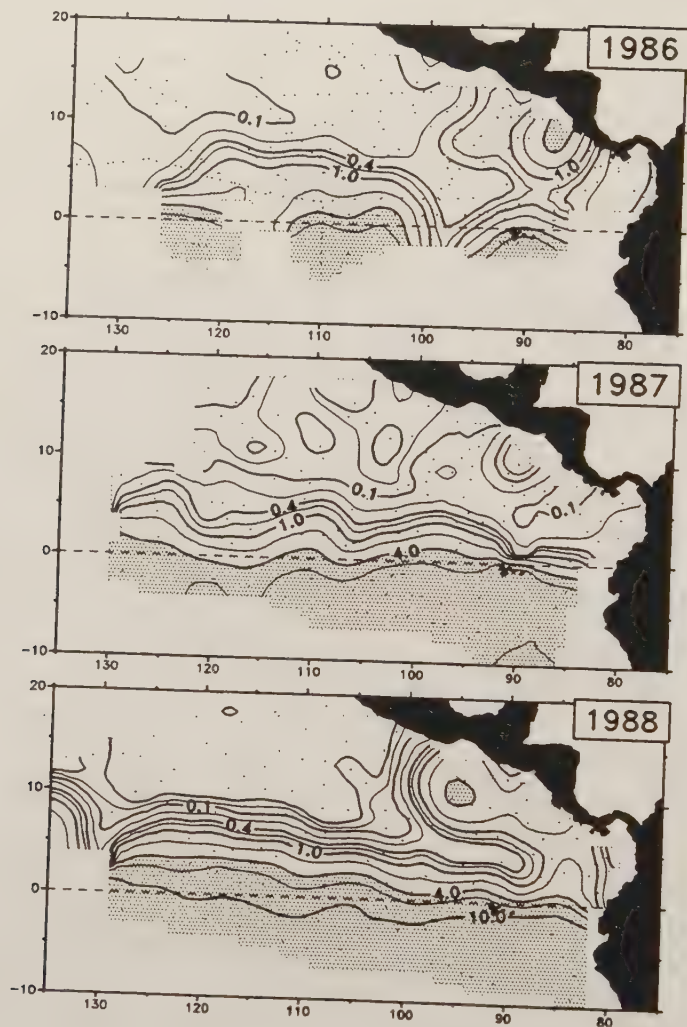


Fig. 6. Surface nitrate concentration ($\mu\text{g-at l}^{-1}$), August–November 1986, 1987 and 1988.

Nutrients supplied by equatorial upwelling sustained high chlorophyll standing stocks in a shallow euphotic zone south of 5°N , with concentrations increasing toward the coast of Ecuador and Peru (Figs 8 and 9). A band of high chlorophyll values extended approximately south of the Gulf of Tehuantepec in southern Mexico (16°N , 94°W), west of the elevated surface nutrients over the Costa Rica Dome. Euphotic zone nitrate concentrations were also high along 10°N . The lowest nitrate concentrations in this band occurred at the thermocline ridge saddle observed at $110\text{--}115^{\circ}\text{W}$. Chlorophyll concentrations were low in tropical water away from the influence of upwelling, decreasing to the west towards the oligotrophic North Pacific subtropical gyre.

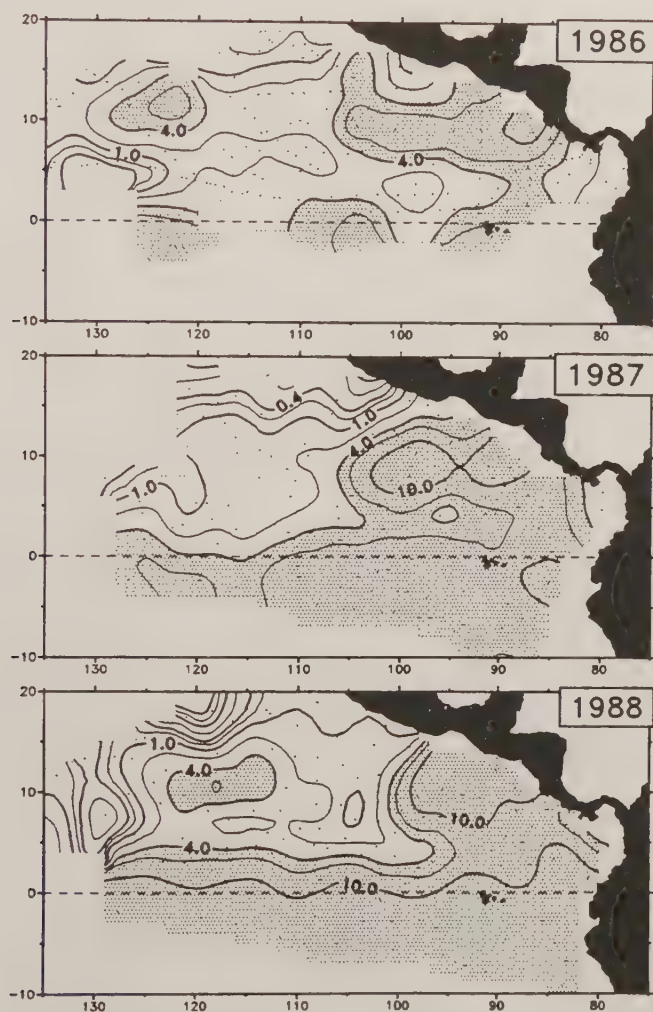


Fig. 7. Mean nitrate concentration ($\mu\text{g-at l}^{-1}$) in the euphotic zone, August–November 1986, 1987 and 1988.

In August–November 1987, surface nitrate concentrations were lower than in 1986 (Table 4). The greatest observed reductions in surface nutrients occurred in tropical water east of 105°W , where surface nitrate concentrations were less than half those observed in 1986. Overall, euphotic zone nitrate concentration did not change significantly between 1986 and 1987. However, the euphotic zone nitrate maximum band along the counter-current thermocline ridge extended only out to about 105°W in 1987 (Fig. 7). Concentrations in this band east of 105°W were higher than at the equator.

Chlorophyll concentrations were lower and the euphotic zone was deeper in 1987 than in 1986 (Table 5). The reduction in chlorophyll was greatest in equatorial water, especially

Table 4. Surface and mean euphotic zone nitrate concentrations ($\mu\text{g-at l}^{-1}$) and interannual ratios for the eastern tropical Pacific study area, August–November (medians of 2° square gridded means). The 1986 medians are biased by undersampling of equatorial water

Year	Surface	Euphotic zone
1986	(0.19)	(2.51)
1987	0.26	5.54
1988	1.13	5.80
1987/1986	0.52***	1.13
1988/1987	1.63***	1.60***
1988/1986	0.48***	1.35

Interannual differences tested by Wilcoxon signed ranks test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

west of 105°W , and in tropical water between 5 and 10°N west of 90°W , along the countercurrent thermocline ridge.

In August–November 1988, surface and mean euphotic zone nitrate concentrations were higher than in 1987 (Table 4). The greatest surface nitrate increases occurred in Central American coastal waters and in equatorial water west of 100°W . Surface nitrate concentrations, within the area north of the equator sampled in 1986, were surprisingly lower in 1988. Chlorophyll concentrations were higher and the euphotic zone was more shallow in 1988 than in 1987 (Table 5). The greatest surface chlorophyll increases occurred in the upwelling systems along the equator near the Galapagos and in coastal waters near

Table 5. Median surface chlorophyll concentrations (mg m^{-3}) and interannual ratios, and mean euphotic zone depths (m) and interannual differences for the eastern tropical Pacific study area, August–November

Year	Surface chlorophyll	Euphotic zone	
		Chlorophyll	Depth
1986	0.18	0.23	60.2
1987	0.13	0.19	69.2
1988	0.21	0.28	54.4
1989	0.19	0.25	58.0
1987/1986	0.77***	0.85***	+8.6***
1988/1987	1.65***	1.58***	-15.4***
1989/1988	0.89***	0.90***	+4.1***
1989/1986	1.14***	1.10***	-2.2***

Interannual differences tested by Wilcoxon signed ranks test (chlorophyll) or paired *t*-test (euphotic zone depth): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

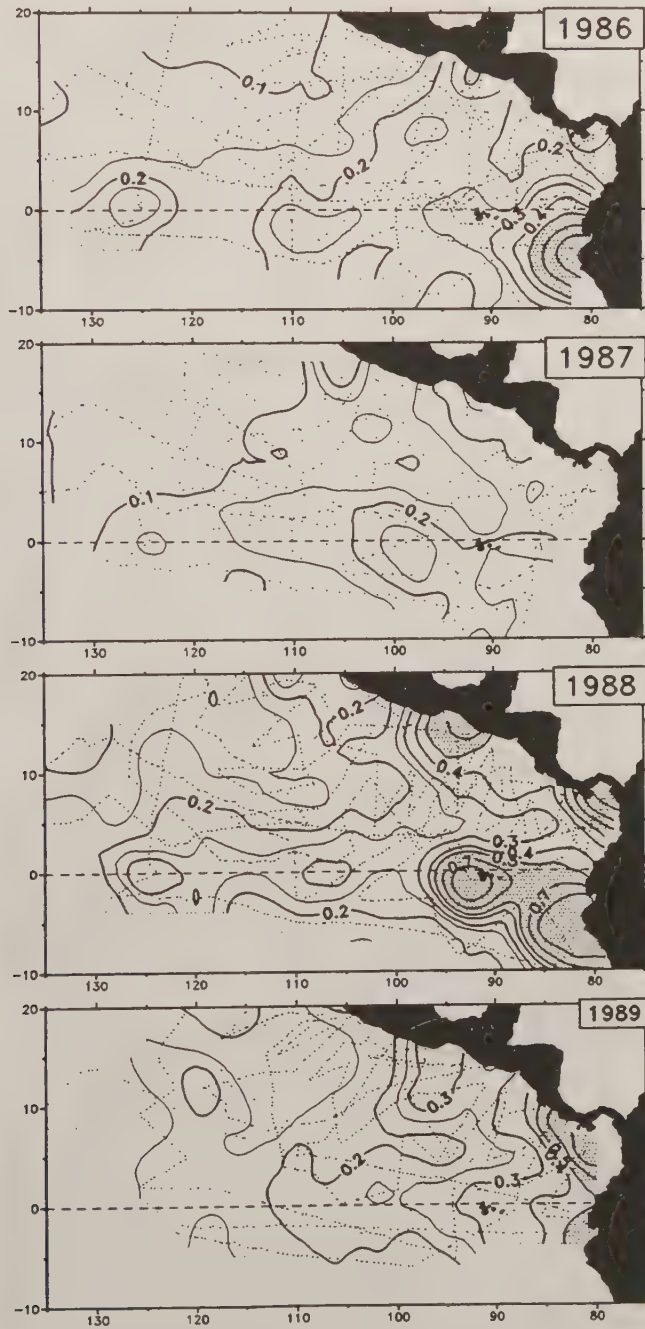


Fig. 8. Surface chlorophyll concentration (mg m^{-3}), August–November 1986, 1987, 1988 and 1989.

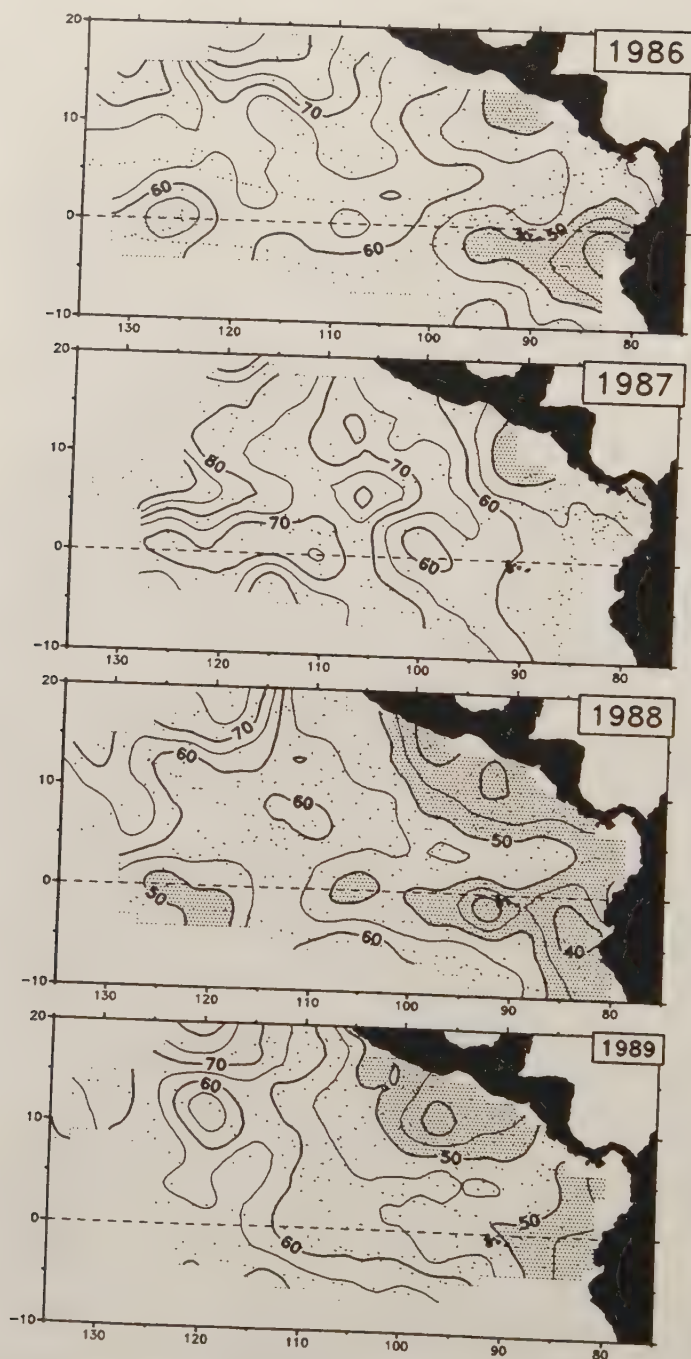


Fig. 9. Euphotic zone depth (m), calculated from phytoplankton pigment profiles (MOREL, 1988), August–November 1986, 1987, 1988 and 1989.

the Gulf of Tehuantepec and in the Gulf of Panama. Increases in subsurface chlorophyll, indicated by a decreasing euphotic zone depth, were greatest to the west of 110°W , where euphotic zone nitrate increased.

In August–November 1989, chlorophyll concentrations were lower and the euphotic zone was deeper than in 1988 (Table 5). The greatest changes occurred in equatorial water and along the coast of Central America north of 10°N . Compared to 1986, chlorophyll concentrations overall were still slightly elevated and the euphotic zone was shoaled by 2 m in 1989.

DISCUSSION

Physical effects

We observed the beginning of an El Niño event in the ETP in August–November 1986: anomalously warm surface temperatures and a depressed thermocline in equatorial water west of 100°W and off the coast of Peru. In terms of the composite ENSO (RASMUSSEN and CARPENTER, 1982), these months would include the “Antecedent Phase” and just precede the “Onset Phase” of an ENSO event reaching its full development in 1987. The composite SST anomaly field shows positive values confined south of 10°S in the ETP for this phase. Only during the “Peak Phase” in the following spring does the composite SST anomaly field show positive values along the equator. In terms of the annual cycle of the SST field, warming along the equator should occur during the spring, beginning in the east and propagating westward. At this stage, the 1986–1987 event appears to be leading the composite event by 3 months (LANDER, 1989; KOUSKY and LEETMAA, 1989). Also, the warming of the surface waters in the ETP does not appear to be a simple enhancement of the annual cycle.

By late 1987, the Southern Oscillation Index had begun to return to normal and the eastern equatorial Pacific SST anomaly had reached a maximum (Fig. 3). We observed anomalously warm surface temperatures throughout the study area, with the warmest anomalies in equatorial water. Thermocline topography was generally flatter than normal. The slope between the countercurrent thermocline trough and ridge (5 – 10°N) was reduced, suggesting a weakened North Equatorial Countercurrent. WYRKTI (1974) showed that the NECC was anomalously strong in the central Pacific during El Niño years, but we did not sample the “peak” phase of the event when the NECC may have been stronger. In the 1982–1983 El Niño, the NECC was anomalously strong in the early stages of the event, but anomalously weak after December 1982 (MEYERS and DONGUY, 1984; KESSLER and TAFT, 1987).

In terms of the composite ENSO (RASMUSSEN and CARPENTER, 1982), the “Transition Phase” of the event would occur in the months of August–October 1987. For this period, in the ETP, the composite SST anomaly field shows positive values throughout the region south of 10°N , with equatorial values exceeding $+1.5^{\circ}\text{C}$. Composite SST anomalies for the “Mature Phase” occurring a few months later show a similar pattern. Our 1987 observations are consistent with these patterns. In terms of the annual cycle, the months of August–November encompass the warmest time of the year for SSTs in the tropical surface water and the coolest time for SSTs in the cold equatorial tongue. Along with the weakened NECC, this would account for the warmer surface temperature anomalies in equatorial water.

The "Mature Phase" of the composite ENSO ends abruptly with a rapid decline of coastal SST anomalies early in the year following the event (RASMUSSEN and CARPENTER, 1982). In the first 4 months of 1988, the eastern equatorial Pacific SST anomaly declined from more than $+1$ to less than -1°C (Fig. 3). We observed anomalously cool surface temperatures and a shallow thermocline over most of the study area, especially in equatorial water west of 100°W . This indicates strengthened SEC flow and equatorial upwelling. The unusually steep zonal thermocline slope north of the equator suggests a strengthened southward flow of cool California Current water into the ETP, which may have contributed to the negative SST anomalies in tropical water during La Niña 1988.

The 1986–1987 El Niño event was less intense than the 1982–1983 event in terms of anomalies in surface temperature, near-surface flow and winds (Fig. 3; McPHADEN and HAYES, 1990). Both events began similarly, with warm SST anomalies developing in mid-year in the central Pacific, prior to the South American coastal warming (KOUSKY and LEETMAA, 1989). Both events were terminated in the ETP by wind events in the central and western Pacific. However, the 1986–1987 El Niño event lasted longer (18 months compared to 12 months in 1982–1983) and was followed by a more intense La Niña event.

The most nearly normal (average) year in this study was 1989 for ETP surface temperature and thermocline depth. By the end of the year, the surface layer of the western equatorial Pacific was anomalously warm and deep. Westerly trade wind anomalies and increased convective activity in the western and central Pacific suggested an incipient El Niño event (KOUSKY, 1990). However, the event had not developed in the ETP by the end of 1990.

Biological effects

Previous studies of the biological effects of ENSO variability, at the primary producer level, have relied on data from single equatorial or coastal transects or stations (DANDON-NEAU and DONGUY, 1983; BARBER and CHAVEZ, 1983, 1986; KOGELSCHATZ *et al.*, 1985). Our data provide the first large-scale view of the biological effects of interannual ENSO variability in equatorial, tropical and coastal waters of the eastern tropical Pacific.

Surface nitrate concentrations in the ETP are highest in equatorial and coastal upwelling regions (Fig. 6). Warm tropical water, beyond the influence of upwelling, has very low nitrate concentrations at the surface. However, mean euphotic zone nitrate concentrations are relatively high in tropical water along 10°N , at the countercurrent thermocline ridge, where the euphotic zone extends below the thermocline (compare Figs 5 and 9). Euphotic zone nitrate concentrations at the countercurrent thermocline ridge are often equal to or greater than values at the equator (Fig. 7). Surface chlorophyll levels are not elevated above this ridge (Fig. 6). However, the euphotic zone deepens over the countercurrent thermocline trough north of the equator and then shoals at the ridge (Fig. 9), suggesting that nutrient input results in increased chlorophyll below the surface.

Upwelling of limiting nutrients from below a shallow thermocline results in high levels of new production in the eastern equatorial Pacific and in Peru coastal waters. Productivity of equatorial and coastal upwelling waters is reduced during El Niño because the thermocline is depressed below the depth of entrainment, so that the upwelled water is warm and depleted of nutrients (BARBER and CHAVEZ, 1986; BARBER and KOGELSCHATZ, 1990). In addition, upwelling-favorable winds (easterly trades) along the equator are reduced (Fig. 3). The greatest relative reductions in nutrient availability between 1986 and 1987 were

observed in tropical water north of the equator. However, the most critical change for phytoplankton productivity is represented by changes in the extent of nutrient-rich water ($>4 \mu\text{g-at l}^{-1}$ nitrate). Equatorial waters remained nutrient-rich in 1987, although nutrient-rich conditions did not extend north of the equator.

We observed a reduction in chlorophyll standing stock that could have been caused by depression of the thermocline during El Niño, leading to reduced transport of nutrients to the surface and lower biological productivity. The equatorial and countercurrent thermocline ridges were anomalously deep in 1987 (Fig. 5), reducing nutrient input from below the thermocline. However, nitrate concentration in equatorial water did not become limiting in 1987, at least in our August–November observations. The equatorial thermocline ridge actually shoaled west of 105°W between fall 1986 and fall 1987. The only part of the study area where we observed a change from nutrient-rich to nutrient-poor conditions was in subsurface waters along the countercurrent thermocline ridge west of 105°W (Fig. 7). BARBER and CHAVEZ (1983, 1986) observed nutrient-depleted water along the equator and 5°S to the coast of Peru in April and May 1983. Normal, nutrient-rich conditions had returned by the next observations in November and July, respectively. Thus, we may have missed a more pronounced thermocline depression and nitrate reduction in equatorial water earlier in 1987.

The countercurrent thermocline ridge normally lies as close to the surface as the equatorial ridge to the south at the same longitude, except at the 100 – 110°W saddle (Fig. 2). Euphotic zone nutrient concentrations above this ridge are as high as at the equator, although nutrients are depleted at the surface (Figs 6 and 7). We observed chlorophyll reductions in this region as great as at the equator (by as much as 50% between 1986 and 1987). These reductions can be explained by observed thermocline depression and lower nutrient availability. However, the pelagic ecosystem over this ridge is functionally different than the equatorial ecosystem: surface nutrient concentrations and chlorophyll standing stock are very low (surface waters more oligotrophic than eutrophic), although enhanced zooplankton standing stocks comparable to those at the equator have been observed (BRANDHORST, 1985; REID, 1962).

We observed major changes in nutrient availability between El Niño 1987 and La Niña 1988. The thermocline shoaled by 20 m or more along both the equator and the Central American coast (Fig. 5), where the greatest surface nitrate increases occurred. Nutrient-rich ($>4 \mu\text{M}$ nitrate) surface water extended up to 400 km north of the equator (Fig. 6). Surface and euphotic zone nitrate concentrations exceeded $10 \mu\text{g-at l}^{-1}$ in equatorial water. Chlorophyll concentrations increased greatly, especially in the upwelling systems along the equator and in Central American coastal waters.

These results are consistent with increased productivity caused by increased upwelling of nutrient-rich water from below the shoaled thermocline/nutricline during La Niña. If El Niño and La Niña are complementary extremes in a cycle of variable biological productivity in the ETP, then the 1988/1987 change lends additional support to the hypothesis that reduced chlorophyll concentrations in 1987 were the result of productivity limited by anomalously low nutrient input in coastal and equatorial upwelling regions.

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The Egg Production Method applied to the spawning biomass estimation of sardine, *Sardina pilchardus* (Walb.), on the North Atlantic Spanish coast

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ABSTRACT

During April-May 1988, an Egg Production Method Cruise was carried out with the purpose of evaluating the spawning biomass of the sardine, *Sardina pilchardus* (Walb.), from the Galician and Cantabrian coasts of Spain. This cruise was coordinated with the acoustical evaluation of this stock on board the R/V Cornide de Saavedra.

The area covered extends from the Spanish-Portuguese border (41° 55' N) to the Spanish-French border (1° 58' W). Vertical plankton tows at 524 stations were distributed over the continental shelf and slope water in a 6×6 mile grid, with a 6×3 mile grid in areas of more intense spawning, to estimate the daily egg production parameter.

A total of 44 epipelagic trawls were done in order to estimate the biological parameter relative to the adult population, that is, average female weight, batch fecundity, spawning fraction and sex ratio.

The survey area was post-stratified into three regions and the spawning biomass was estimated for each region. The sum of the three spawning biomass estimates was the total spawning biomass for the survey area. Three regions were established by differentiated adult parameters, such as average female weight in conjunction with the considered acoustical divisions. These regions correspond to the Galician coast (I), the western Cantabrian area (II) and the eastern sector of the Cantabrian coast (III).

The biomass estimates with their respective coefficient of variation of each region were as follows:

	Galicia I	W Cant. II	E Cant. III	Total Areas
Spawning Biomass (B)	134 195	33 503	12 467	180 165
CV	0.66	0.30	0.56	0.50

Maximum biomass estimates were found on the Galician shelf, although the stock was mainly concentrated in the northern sector of Galicia and the westernmost part of the Cantabrian shelf. Biomass estimates decreased towards the east. The trend in spawning biomass was similar to the total biomass estimate from the acoustic survey, with a total estimate of 174 016 t.

Key words: sardine, evaluation, egg production, fecundity, Cantabrian Sea, Spain.

RESUMEN

El Método de Producción de Huevos aplicado a la estimación del stock reproductor de sardina, *Sardina pilchardus* (Walb.), en aguas noratlánticas españolas.

Desde abril a mayo de 1988 se aplicó el Método de Producción Diaria de Huevos con el objetivo de estimar la biomasa reproductora de la sardina noratlántica española, *Sardina pilchardus* (Walb.), comprendida en el área de las costas de Galicia y del Cantábrico. Esta campaña fue realizada coordinadamente con la campaña de evaluación acústica de pelágicos a bordo del B/O Cornide de Saavedra.

El área de cobertura se extiende desde la frontera luso-española ($41^{\circ} 55' N$) hasta la frontera con Francia ($1^{\circ} 58' O$). Se muestrearon 524 estaciones para la recogida de muestras planctónicas a lo largo de la plataforma y talud en un mallaje de estaciones de 6×6 millas náuticas, y en zonas de mayor abundancias de huevos en 6×3 , con el propósito de estimar la producción diaria de huevos de sardina.

Se llevaron a cabo un total de 44 pescas epipelágicas con el fin de estimar los parámetros biológicos y reproductivos de la población de adultos, como son el peso medio de las hembras, fecundidad parcial, fracción de hembras en puesta y proporción de sexos.

El área muestreada fue post-estratificada en tres regiones y, consiguientemente, la biomasa reproductora estimada para cada una de las mismas. La biomasa reproductora total se logra con la suma de cada una de las biomásas por región. El criterio de estratificación por regiones se basa en la diferenciación zonal de los parámetros de adultos, como es el peso medio de las hembras, coincidiendo con las divisiones acústicas preestablecidas. Estas regiones corresponden a las costas de Galicia (I), Cantábrico occidental (II) y Cantábrico oriental (III).

El resultado de las estimaciones de la biomasa reproductora de sardina junto con sus respectivos coeficientes de variación figuran a continuación:

	Galicia I	Cant. oeste II	Cant. este III	Total Areas
Spawning Biomass (B)	134 195	33 503	12 467	180 165
CV	0.66	0.30	0.56	0.50

El máximo de biomasa se produce en las costas norte de Galicia y la parte más occidental del Cantábrico. La biomasa tiene una tendencia decreciente hacia el este, igualmente acusables por acústica, que estima el stock en 174 016 t.

INTRODUCTION

Fisheries assessment and management on the Iberian pilchard, *Sardina pilchardus* (Walb.), from the North Atlantic coast have been used with two stock evaluation methods: VPA (since 1976) and acoustic survey evaluations (since 1983). Within the framework of a SARP project on sardine recruitment variability, another stock estimation procedure, the Daily Egg Production Method (DEPM), was introduced (Lasker, 1985). The DEPM has been used for the spawning biomass estimates of northern anchovy, *Engraulis mordax*, off California (Picquelle and Hewitt, 1983; Picquelle and

Hewitt, 1984; Bindman, 1986; Smith and Hewitt, 1985). It has also been used for related species, such as the Peruvian anchovy, *Engraulis ringens* (Santander; Alheit and Smith, 1984), and the southern Benguela anchovy, *Engraulis capensis* (Armstrong et al., 1988). In the ICES area, efforts are being made to apply fishery-independent estimates such as the DEPM. Alheit (1985) described the method at the ICES 73rd Statutory Meeting. Santiago and Sanz (1989) applied DEPM to the Bay of Biscay anchovy *Engraulis encrasicolus*.

The purpose of this paper is to present the first experience of DEPM on the Iberian sardine (*Sardina pilchardus*). A DEPM cruise

combined simultaneously with an acoustic survey covered the whole of the Galician and Cantabrian waters. This survey was coordinated with another DEPM survey along the Portuguese coast on the same species (Cunha *et al.*, 1989).

To conduct a successful DEPM cruise, the following information is required: the spatial and/or temporal distribution of the egg stages of pilchard and the delimitation of the spawning areas (Smith and Hewitt, 1985).

The survey was conducted during the peak spawning period (from March to April) (Dicenta, 1984; Solá, 1987; Lago de Lanzós, Franco and Solá, 1988; Pérez *et al.*, 1985; García *et al.*, 1988).

The knowledge of the reproductive biology of pilchard and the correct histological techniques are also essential for obtaining accurate estimates of the reproductive parameters.

MATERIAL AND METHODS

Survey description

The combined DEPM and acoustic survey of 1988 (MPH Saracus 0488) was conducted aboard the R/V Cornide de Saavedra from March 29 to May 6. The cruise began in the southern area of the Galician shelf next to the Spanish-Portuguese border (41° 55' N, 08° 55' W) and ended in the transect close to the Spanish-French border (43° 43' N, 1° 58' W) (fig. 1).

A 6 × 6 mile grid was the basic plankton station scheme. Transects were spaced every 6 miles and acoustic tracking was carried out following the stations' numerical order. To achieve a more precise estimate of egg production, other plankton tows were conducted in the western and part of the eastern Cantabrian area, where high spawning activity occurred. The 6 × 6 mile grid was modified to a 6 × 3, that is, adding up one station every 3 miles within the same transect. There were 524 plankton stations representing a coverage of 51 736 km² of sea surface. Sardine eggs were present at 283 stations.

Plankton samples were taken using a 25 cm diameter net of 150-micron mesh (Smith,

Flerx and Hewitt, 1985) retrieved vertically from a depth of 100 m at a speed of approximately 1 m/s. The mean volume filtered was 5.09 m³ with a standard deviation of 1.05 m³.

In every station, surface temperature, wind speed and direction were recorded. Salinity, temperature, depth (CTD) (77) and expendable bathythermography (XBT) (50) casts were conducted at about 25% of the stations sampled.

Adult sardine were sampled with an epipelagic trawl at 30 sampling stations out of 44 tows (fig. 2), and 7 of them showed hydrated females. The sampling strategy followed a judgment sonar sampling of sardine schools along the coastline. We estimated the total number and weight of sardine caught.

Fish were processed on board with random sampling, in each trawl: 50 fish served to record sex and maturity and to measure standard length to determine sex ratios. Gonads of 25 obvious females and 10 males were frozen. The gonads of all hydrated females captured ($n=116$) were preserved and the ovary-free body frozen.

Egg production estimation model

The spawning biomass estimate was based on Parker's (1980) equation on biomass estimation, modified by Stauffer and Picquelle (1980) for the northern anchovy, *Engraulis mordax*:

$$B = \frac{kAP_0W}{RFS}$$

where,

- B = spawning biomass in metric tons
- P_0 = daily egg production (number of eggs per sampling unit, 0.05 m²)
- W = average weight of mature females (g)
- R = sex ratio (fraction of mature females by weight)
- F = batch fecundity (mean number of eggs per mature female per spawning)
- A = total survey area (in 0.05 m² sampling units)

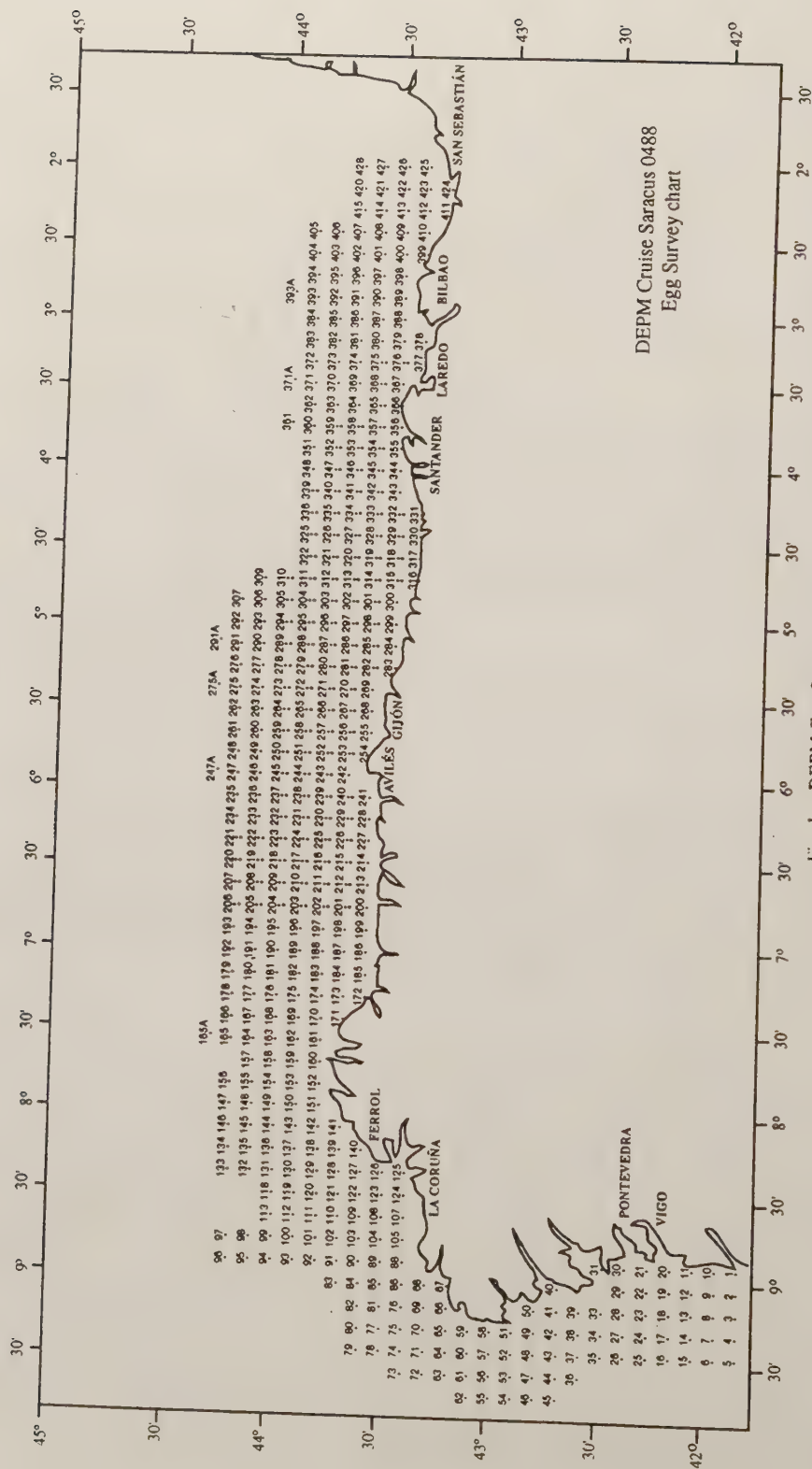


Fig. 1.—DEPM Egg Survey chart.

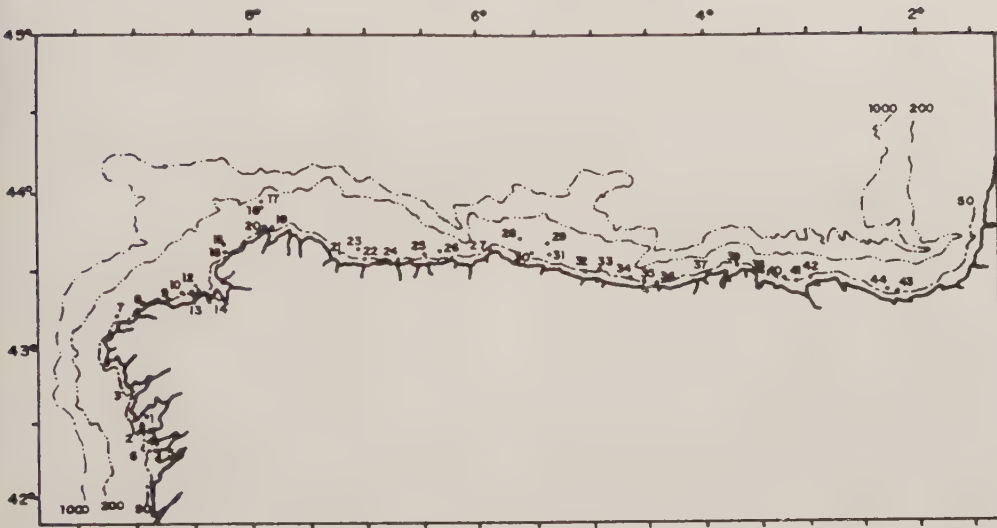


Fig. 2.—Adult trawl survey chart.

Fig. 2.—Mapa de estaciones de muestreos de adultos.

S = fraction of mature females spawning per day
 k = conversion factor from grams to metric tons

The variance of the biomass estimate through this method is calculated by the delta method (Seber, 1973), as a function of variance and covariance of the estimates of parameters:

$$\begin{aligned} \text{Var}(B) = B^2 \cdot & \left[\frac{\text{Var}(P_0)}{P_0^2} + \frac{\text{Var}(W)}{W^2} + \right. \\ & + \frac{\text{Var}(R)}{R^2} + \frac{\text{Var}(F)}{F^2} + \frac{\text{Var}(S)}{S^2} + \\ & + 2 \left(\frac{\text{Cov}(P_0, W)}{P_0 W} - \frac{\text{Cov}(P_0, R)}{P_0 R} - \right. \\ & - \frac{\text{Cov}(P_0, F)}{P_0 F} - \frac{\text{Cov}(P_0, S)}{P_0 S} - \frac{\text{Cov}(W, R)}{W R} \\ & - \frac{\text{Cov}(W, F)}{W F} - \frac{\text{Cov}(W, S)}{W S} + \frac{\text{Cov}(R, F)}{R F} + \\ & \left. \left. + \frac{\text{Cov}(R, S)}{R S} + \frac{\text{Cov}(F, S)}{F S} \right) \right] \end{aligned}$$

Daily egg production in the survey area, $P_0 A$, is based on the egg sampling and a temperature-dependent model of the sardine egg developmental rate, while the biological parameters of the adults are estimated from the adult sampling trawl survey.

RESULTS

Egg distribution pattern

Sardine fish egg distribution is shown in figure 3. No spawning activity was observed in the southernmost area of the Galician region. Spawning was first registered south of Cape Finisterre in the mouth of Ría de Arosa (transect lines 31-35), and continued toward the northwest-east direction. Actually, the area of these first egg catches coincided with the first adult catches, which contained the first samples of females with hydrated oocytes.

The distributional pattern indicates regional differences, which were taken into account in this study. In the Galician region, spawning areas of pilchard are restricted to the coastal areas, whereas in the western and central Cantabrian (Asturian region)

pilchard eggs are widespread and extend to offshore waters (García, Franco and Solá, 1992) and in some transects (between Avilés and Gijón), the spawning area was not encompassed with negative egg hauls. The eastern Cantabrian seems to show an intermediate situation, with a higher predominance of a more littoral type of distribution of pilchard eggs.

In general, the distribution of adults — whether measured by sonar mapping or by the size of sardine catches — coincides with that of the eggs, except in offshore areas of the western Cantabrian.

Significant differences in the adult biological parameter estimates and differences in egg distribution and the preestablished acoustical divisions led us to post-stratify the survey area into three regions (I, II and III), and the DEPM spawning biomass estimate was obtained for each region. Region I corresponds to the Galician area, extending from the south ($41^{\circ} 55' N$) to the north, including a section of the western Cantabrian (transect lines 179-185).

Region II covers the western Cantabrian; egg presence dominates most of this area. This region includes from transect lines 186-192 to transect lines 351-355.

Region III, the eastern Cantabrian, was the smallest area.

DEPM Parameters Estimate

Daily Egg Production, P_0

The parameter P_0A , the daily production of eggs in the sea, is the total area multiplied by the number of eggs spawned per day per unit area, averaged over the range

and duration of the survey, or in this case, within each of the regions considered.

Positive plankton tows provided the sardine egg data and eggs were staged and aged. Egg production, P_0 , is estimated by fitting an exponential mortality function to the data of eggs at age. Time-zero intercept of the fitted function is the estimate of egg production at spawning.

Following the sampling scheme used by Picquelle and Hewitt (1983) for northern anchovy, the total area was first determined by the sampled surfaces in terms of 6×6 n mi grid. A 0.05 m^2 sampling unit represents the center of this block. This sampling design assumes that the distribution of eggs within one block is independent of the distribution within the adjacent blocks. In the areas of expected spawning intensity, sampling intensity increased to a 6×3 n mi grid. In order to compensate for this uneven sampling intensity, each station was assigned a weighing factor, proportional to the area which the station represents.

Secondly, the stations were stratified by location in order to decrease variance. Many stations were located beyond the spawning range of pilchard. These contribute a large number of stations with 0 egg counts. To reduce their impact on variance, the total survey area was poststratified into two strata: stratum 0 contains the geographical area where no spawning occurs (thus, daily egg production = 0) and stratum 1 includes the stations where positive egg counts occurred, along with the few negative stations imbedded in this area. These two strata were created for each region (fig. 3).

Their respective areas (km^2) and the number of stations (n) comprising each stratum by region were as follows:

Stratum	Galicia I	W Cant. II	E Cant. III	Total areas
I 1 Area (km^2) n	6 915 56	13 829 186	5 680 41	26 424 283
0 1 Area (km^2) n	15 188 123	6 668 81	3 457 37	25 313 241
Total Area n	22 102 179	20 497 267	9 137 78	51 736 524

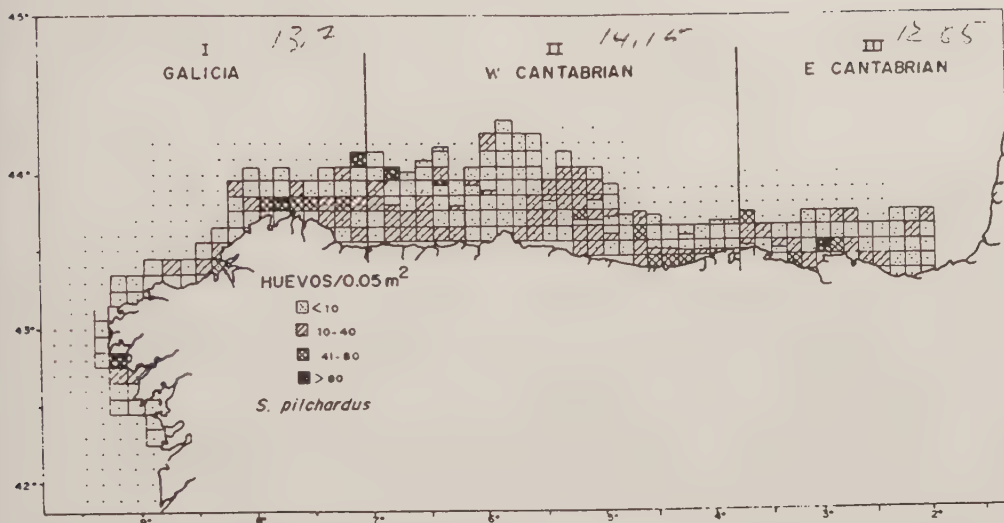


Fig. 3.—Sardine egg abundances (eggs/0.05 m²) by regions. Shaded blocks represent the positive stratum.

Fig. 3.—Abundancias de huevos de sardina (huevos/m²) por regiones. Bloques sombreados corresponden al estrato positivo.

Sardine eggs from each sample were counted and staged according to their degree of embryonic development. These were classified into the 11 stages established by Gamulin and Hure (1955), complemented with criteria described by Moser and Ahlstrom (1985) and Ahlstrom (1943). These stages of eggs were then aged.

The stage-to-age procedure was based on the results of a laboratory experiment, in which the induction-spawned eggs were incubated at five temperatures (11° C, 13° C, 15° C, 18° C and 20° C) and the elapsed times were recorded (Miranda, Cal and Iglesias, 1989).

Analysis of the empirical data on the rate of development indicated that the best fit of development curves was the combination of an exponential and power function, described in Lo (1985).

The resulting equation was:

$$Y_{i,t} = 17.515 e^{-1.13621(t) - 1.1734(i)} i^{2.222}$$

where,

$y_{i,t}$ corresponds to the average age of the egg at stage i and temperature t . It showed a very good fit; r^2 was 0.986.

Thus, for each of the 11 stages, the average age of sardine eggs can be estimated

from the above equation for a given temperature.

The program STAGEAGE described in Hewitt, Bindman and Lo (1984) and in Lo (1985) was modified according to 1) a model for a temperature-dependent egg development, 2) the distribution of age within each stage, and 3) a daily peak spawning time (19:00 GMT), in order to acquire an automated ageing procedure.

The STAGEAGE, a FORTRAN program, was compiled to run on a compatible PC. It was modified and named SSTAGEAG, with reference tables that allow the assignment of ages to the egg data set according to the station temperature and the time of tow. These reference tables were created assuming peak spawning time at 19:00 GMT, and thus measure the time elapsed between spawning and catch.

STAGEAGE outputs several data files (Lo, 1985), among which FOR038.DAT gives the results of two variables, number of eggs and age in day categories, A, B, and C-day eggs. Thus, the data is tabulated by age for each station, with each one accounting for up to three observations (one for each day category). This file was used directly for the regression estimates of egg production and egg mortality rates.

The exponential mortality model

$$P_t = P_0 e^{-zt}$$

was then fit to the data using a weighted nonlinear least squares regression (Dixon and Brown, 1979), where,

P_t = number of eggs per 0.05 m² in age category t

t = age in days measured as the elapsed time from the spawning to the time of sampling

P_0 = daily egg production per sampling unit (0.05 m²)

z = daily rate of instantaneous mortality

This model was fit to the data from stratum 1 for each of the three regions. In consequence, each region has an estimate of P_{01} (intercept) and a corresponding egg mortality, z (slope) (fig. 4).

The final stratified estimate of P_0 by regions was calculated as the weighted average of the two strata, where the strata weights u_i are proportional to A_i , the area of the i th stratum and P_{00} is zero by definition,

and the weights are the relative areas of the two strata, that is,

$$u_i = \frac{A_i}{A_1 + A_0}$$

$$P_0 = u_1 P_{01} + u_0 P_{00} = u_1 P_{01}$$

and the variance, adjusted for the postsurvey stratification (Jessen, 1978), is:

$$\text{Var}(P_0) = \left(1 + \frac{1}{n}\right) \left[\left(\frac{A_1}{A}\right) \text{Var}(P_{01}) + \left(\frac{A_0}{A}\right) \text{Var}(P_{00}) \right]$$

where, A_i is the area of stratum i for each region, n is the total number of observations by region, $\text{Var}(P_{01})$ is the estimated variance of stratum 1 for each region as calculated from the regression, $\text{Var}(P_{00})$ is zero by definition.

Figure 5 represents the fitted curve of egg

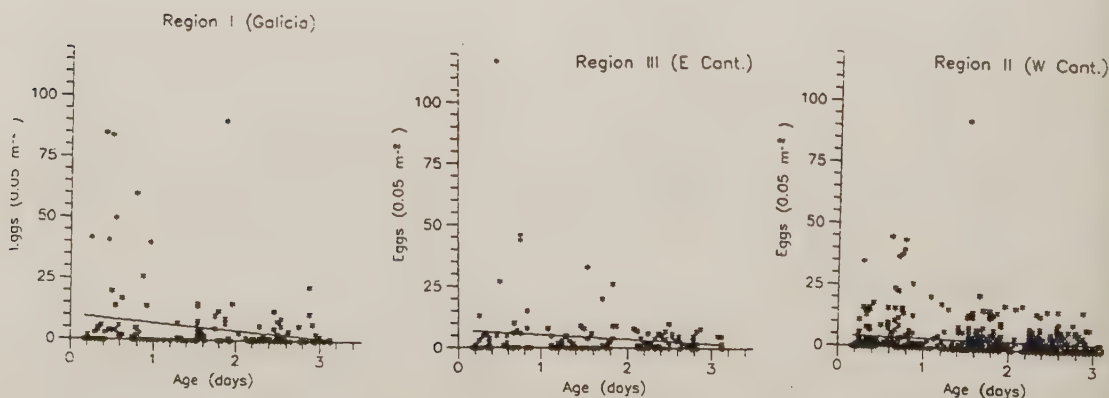


Fig. 4.—Exponential mortality model for estimating P_{01} plotted with egg abundances for each region, where P_{01} is the daily egg production at Day-0 in stratum 1.

Fig. 4.—Curvas de ajuste a función exponencial para la estimación de P_{01} con la abundancia de huevos por región, en la que P_{01} representa la producción diaria de huevos en el día 0 en estrato 1.

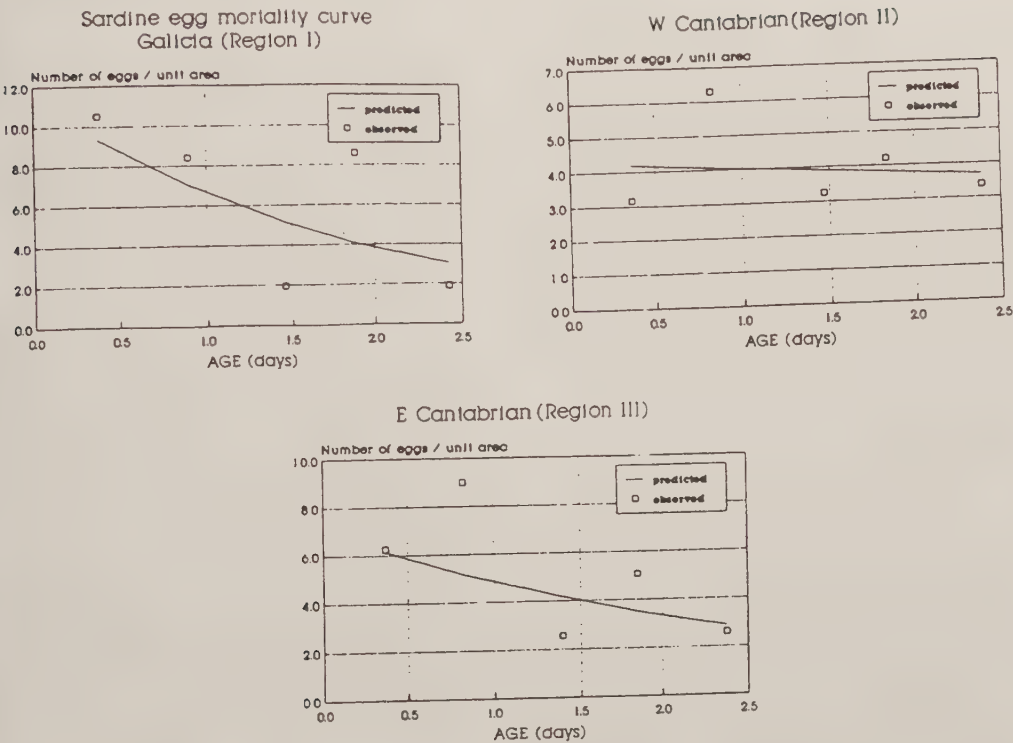


Fig. 5.—Egg mortality curves for each of the regions plotted as mean abundance by half-day intervals.
Fig. 5.—Curvas de mortalidad de huevos por región representados por la abundancia media en intervalos de medio día.

production rates for each of the regions computed in mean half-day frequencies of age.

In summary, the results related with the estimates of P_{01} and P_0 , for the three regions were:

Region I had the highest egg densities, P_{01} , due to the high egg counts that occur on the northern coast of Galicia and the westernmost coast of the Cantabrian region. On the other hand, in region I, P_0 drops to values similar to those produced in re-

Stratum	Galicia I	W Cant. II	E Cant. III
P_{01} (eggs/0.05 m ²) Standard error	11.52 3.78	4.29 0.86	7.08 3.02
z (egg mortality) Standard error	0.55 0.33	0.062 0.14	0.38 0.38
u_0 u_1	0.69 0.31	0.33 0.67	0.40 0.60
Mean Temperature (°C)	13.7	14.15	12.85
P_0 (eggs/0.05 m ²) Standard error	3.5712 2.1046	2.8743 0.7039	4.248 2.3392

regions II and III, because in this region, 31 % of the weighted areas account for the positive stratum, whereas in regions II and III, this relationship is over 60 %. Intense spawning in the Galician area was confined to a rather small area in relation to the total surveyed area. These concentrated high egg densities resulted in the high standard error of the estimate.

In contrast, in the western Cantabrian (II), spawning showed a widespread distribution and the resulting egg counts data set was much more homogeneous.

Adult Parameters

The adult parameters, W , F , S and R , were estimated through the epipelagic trawl samples and the biological sampling of sardines done during the cruise.

Three main problems have to be noted in the adult sampling survey: 1) difficult fishing operations in rocky areas of the northern Galician shelf, 2) inaccessibility to areas where fishing gear of fixed nature was installed (western and eastern Cantabrian) and, 3) hydrated females had to be fished during daylight hours, moments at which sardine are most likely to avoid the net.

In all regions, sardine are restricted to coastal areas, except where high egg abundances occurred in offshore areas, such as the western Cantabrian; but, generally the geographic distribution of adult fish schools observed by the sonar mappings or the adult sardine catches agreed with the distribution of eggs.

For each of the parameters, mean and variance were estimated following Picquelle and Stauffer's (1985) procedure, calculating weighted averages (since the number of sampled individuals were not equal in each of the tows), where,

$$\bar{y} = \frac{\sum_i m_i \bar{y}_i}{\sum_i m_i} \quad (1)$$

$$\widehat{Var}(\bar{y}) = \frac{\sum_i m_i^2 (\bar{y}_i - \bar{y})^2}{\left[\sum_i m_i / n \right]^2 \cdot n / (n - 1)} \quad (2)$$

$\bar{y}$ = the estimate of the population mean
 n = number of collections

$\bar{y}_i = \sum y_{ij} / m_i$ observed mean value in collection i

y_{ij} = observed value for the j^{th} fish sampled and i^{th} trawl

m_i = the number of fish subsampled from the i^{th} catch

Average Female Weight, W

This parameter was calculated as the mean weight of mature females per trawl, using a maximum number of females as subsample target, which was 25 mature females per trawl and a total of 563 females. However, this number was not always reached, because either few fish were caught or most of the catch were immature females.

In the estimation of this parameter y_{ij} of equation (1) becomes W_{ij} , that is, the whole body weight of the j^{th} mature female from the i^{th} trawl. This observed weight has to be adjusted for those females which were in hydrated condition, due to the water retention during hydration. This adjusted W_{ij} was estimated through a linear regression of whole body weight to ovary-free weight for females which had no hydrated oocytes.

The resulting linear regression is:

$$W = -2.051 + 1.079 W^*$$

where,

W is the whole body weight of mature females and,

W^* is the ovary-free weight of females without hydrated eggs.

The following data on this parameter represents the average weight of mature females by regions with their corresponding coefficients of variation, showing a clear increase of this parameter in an eastward direction, in accordance with the differential distribution of the adults mentioned by Porteiro *et al.* (1986).

Av. Female Weight	Galicia I	W Cant. II	E Cant. III
W (g)	64.93	79.34	86.31
CV	0.06	0.08	0.03

Batch Fecundity, F

Hydrated females were collected throughout the survey, and the number of eggs per batch (F) was the basic data set for this parameter. Batch fecundity was estimated by regressing batch fecundity (F) on ovary-free weight of those females which had hydrated oocytes (W^*) and without postovulatory follicles, as shown through histological analysis, indicating that spawning had not begun.

A total of 126 females with hydrated oocytes, obtained from the DEPM survey carried out by Spain and Portugal, were analyzed in order to have a higher number of ovaries for regression analysis, because there were no significant differences in the number of oocytes per gram of fish between specimens from Spain and Portugal (Pérez *et al.*, 1989).

A weighted linear regression was used to estimate batch fecundity of all the mature females up to maximum number of 25 per catch.

The resulting linear regression was:

$$F = -1260.8 + 444.43 W^*$$

The average batch fecundity was calculated from equation (1), but in this case, variance is estimated as described in Draper and Smith (1966), where,

$$Var(\bar{F}) = \frac{\sum_i m_i^2 \cdot \frac{(\bar{F}_i - \bar{F})^2}{n-1} + \frac{S_h^2}{n_h} + (\bar{W}_i - \bar{W}_h) \hat{Var}(\beta)}{\left[\sum_i \frac{m_i}{n} \right]^2 n}$$

where,

- $\bar{F}$ = the estimate of batch fecundity for the whole population of mature females
- $\bar{F}_i$ = the average batch fecundity
- S_h^2 = the variance in regression
- n_h = the number of hydrated females used in the regression
- $\bar{W}_i$ = average ovary-free weight for the i^{th} trawl
- $\bar{W}_h$ = average ovary-free weight for the n_h hydrated females

$\hat{Var}(\beta)$ = the variance of the slope of the regression.

The results of the analysis of this parameter were:

Batch fecundity	Galicia I	W Cant. II	E Cant. III
F	27274.80	33801.80	33910.70
CV	0.06	0.09	0.03

Because batch fecundity is high for larger females, it is expected to observe higher batch fecundity in eastern regions: regions II and III.

Spawning fraction, S

This parameter represents the fraction of mature females that have spawned per day.

Since no validated system existed to classify sardines postovulatory follicles by age, these were assigned to follicles taking into account their histological characteristics, the sample collected time, and maximum intensity of spawning hours. This time was delimited at 19:00 GMT, by the frequency of females with hydrated and postovulatory Day-0 follicles, at different times in the sample caught.

The analysis of the histological age structure of postovulatory follicles of female field samples had revealed the possibility of determining four different ages. An artificial spawning technique for aging sardines' postovulatory follicles (Pérez *et al.*, 1989) was used to confirm the histological criteria applied to the postovulatory follicles of the sea-caught females sampled during the DEPM survey held in 1988. With this experiment, we know that the degeneration of follicles in pilchard has been shown to be very slow; and therefore, follicles are clearly differentiated with ages reaching 80 hours. Females with follicles from 0:00 to 6:00 hours have been classified as Day-0, from 18:00 to 30:00 hours as Day-1, from 42:00 to 54:00 as Day-2 and finally as Day-3, those follicles with ages over 66:00 hours.

The term y_{ij} of equation (1) here is equal to the average proportion of mature females

in the *i*th trawl which have Day-1 and Day-2 postovulatory follicles. Day-2 postovulatory follicles have been included in the estimate, since the degeneration of follicles in pilchard is very slow.

There was an oversampling of follicles under 18 hours (Day-0), thereby causing a bias in the calculation of the spawning fraction. In this manner, the total number of mature females has been calculated following the expression,

$$m_i = \frac{\text{Day-1} + \text{Day-2} + \text{Day-3}}{3} +$$

$$+ \text{Day-1} + \text{Day-2} + \text{Day-3} + \text{Mature females}$$

in which each term represents the number of females in a particular age of postovulatory follicles.

The following table shows the spawning fraction values by the different postovulatory follicle ages by the different regions and their respective coefficients of variation.

The coefficient of variation in relation to the spawning fraction increases as we use the Day-1 or Day-2 postovulatory follicles, instead of their mean value.

Follicle age	Galicia I	W Cant. II	E Cant. III
Day-0	0.64	0.15	0.10
CV	0.58	0.68	0.47
Day-1	0.04	0.09	0.23
CV	0.55	0.24	0.20
Day-2	0.11	0.17	0.19
CV	0.24	0.22	0.20
Day-3	0.05	0.23	0.13
CV	0.60	0.14	0.23
Day-1 + Day-2	0.08	0.13	0.21
CV	0.20	0.11	0.13

The values of spawning fraction by regions also show an increasing trend towards the east, indicating a higher spawning frequency in the older females.

Spawning fract.	Galicia I	W Cant. II	E Cant. III
S	0.8	0.13	0.21
CV	0.20	0.11	0.13

Sex ratio, R

This parameter was calculated as the fraction in weight of mature females of the population. The equation used is also (1), but in this case, m_i is the weight of the subsample instead of the number of fish and y_i is the fraction of the weight of the subsample that corresponds to female fish.

Mature and immature male specimens were included in the analysis. The maximum number of specimens per trawl was 50, from which only the weights of the first 10 males and 25 females were measured.

The total weight for each sex was obtained from Picquelle and Stauffer (1985), where,

$$m_i = W_i^F + W_i^M$$

m_i is the weight of the subsample,
 W_i^F is the total estimated female weight and,
 W_i^M is the total estimated male weight,
and, y_i is the estimated total weight divided by m_i ,

$$y_i = \frac{W_i}{m_i}$$

The results of the estimates of this parameter were:

Sex ratio	Galicia I	W Cant. II	E Cant. III
R	0.35	0.65	0.66
CV	0.12	0.10	0.08

Region I registered low sex ratio values whereas regions II and III recorded estimates of more than 50%. If sex ratio were calculated for the entire survey area, it would be 55%.

Biomass Estimate

All the required parameters for estimating the spawning biomass are summarized in the following table. The biomass estimates

The sample covariances were calculated for the adult parameters, since P_0 was derived from the plankton survey, whereas the adult parameters were derived from the trawl survey. Thus the sample covariance

DEPM Parameters	Galicia I	W Cant. II	E Cant. III
P_0 CV	3.57 0.59	2.87 0.25	4.25 0.55
A (in 0.05 m^2)	4.420×10^{11}	4.099×10^{11}	1.827×10^{11}
W (g) CV	64.93 0.06	79.34 0.08	86.31 0.03
F CV	27274.8 0.06	33801.8 0.09	33910.7 0.03
S CV	0.08 0.20	0.13 0.11	0.21 0.13
R CV	0.35 0.12	0.65 0.10	0.66 0.08
Biomass (B) CV	134 195 0.66	33 503 0.30	12 467 0.56
TOTAL BIOMASS = CV =	180 165 0.50		

of each region were calculated by the egg production estimation equation, and the variances were calculated using the delta method (Seber, 1973).

between P_0 and the adult parameters was assumed to be 0.

The sample covariances calculated for the adult parameters were:

Sample covariance	Galicia I	W Cant. II	E Cant. III
Cov (W, R)	0.01227	0.142	0.0719
Cov (W, F)	5833.1	17783.2	2047.1
Cov (W, S)	0.0156	0.0276	-0.0408
Cov (R, F)	5.484	63.162	30.076
Cov (R, S)	0.00029	0.00024	-0.000469
Cov (S, F)	7.0029	12.31	-17.818

DISCUSSION AND CONCLUSIONS

The DEPM assumes that the parameters in the model are constant over the range and duration of the survey. Since this assumption does not occur in this paper, the spawning biomass of the Galician and Cantabrian pilchard has been evaluated by regions.

One of the clearest differentiations was observed in the mean weight of mature females. An increment towards the east of this parameter is very clear; and it has been demonstrated by Porteiro, Álvarez and Pereiro (1986) that the oldest age classes of pilchard (over 5 years old) mainly reside in the eastern sector of the Cantabrian coast. Different age composition of adult fish affects other parameters, such as batch fecundity, which in the distributional areas of the young age-classes (Galicia) is quite lower.

In the case of sex ratio, the differences between regions are quite pronounced. In Galicia (I), this value is 0.35, in contrast to the two other established regions, where

there is a predominance of females in the population. Different fishing times by regions may ultimately have altered the number of females in the different areas. However, no clear relationship exists between the fraction of reproductive females and trawl time for any of the three regions (fig. 6). The explanation of this phenomenon would be that in part of region I (northern Galician shelf), the difficult fishing operations in rocky areas were bigger than in other regions, and the sardine outside these areas were more vulnerable to the fishing gear. Most of these sardine were spawning, and the proportion of sex at that moment was less, because many males and few females are more effective for reproduction.

Comparing the biomass estimate by the DEPM acoustic evaluation, there is a remarkably slight difference in the total biomass of approximately 6000 t. Porteiro, Miquel and Carrera (1989) had made acoustic estimates of 102 394 t for region I, 58 010 t for region II and 13 612 t for region III.

The general trend among regions be-

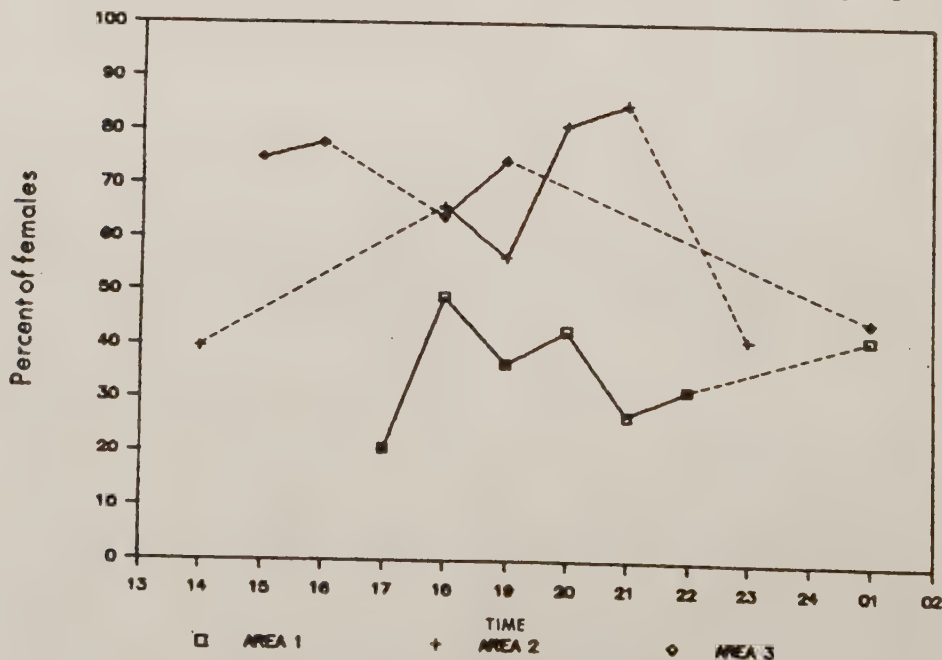


Fig. 6.—Proportion of females by times and regions.

Fig. 6.—Proporción de hembras de sardina por horas y regiones.

tween DEPM and acoustics is similar, showing an increment of biomass from east to west. The adult parameters estimate shows concordance between both methods. For example, acoustic sampling revealed that region I had the principal fraction of age classes 0 and 1, while the DEPM estimates indicated that in this region, batch fecundity, average female weight and spawning fraction were lowest. In the eastern sectors, a greater representation of the older age classes from the acoustics survey was reflected by the estimate of the adult parameters.

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Human-assisted Fostering of Hawaiian Monk Seal Pups

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An unusual feature of Hawaiian monk seal (*Monachus schauinslandi*) reproductive behavior is that lactating females often nurse pups other than their own (Johnson and Johnson 1984, Alcorn and Henderson 1984, Boness 1990). A female apparently becomes confused over the identity of her pup and allows another pup to suckle. However, because females do not have sufficient nutritional reserves to raise more than one pup, the female will usually allow only one pup to suckle at a time. In order to survive, the displaced pup must find another lactating female, and this is frequently the one from which the first pup just came. The net result is an exchange of pups. Such "pup switching" or fostering behavior is more common where the density of mother-pup pairs is high (D.J. Boness, pers. comm.).

Why such a "loose" system of pup recognition should have evolved is an interesting question. Perhaps there has been little selection for accurate pup recognition because there was little need for it. True to their name, monk seals are solitary animals, and do not form the dense colonies that characterize other pinniped species. Widely scattered mothers are less likely to encounter other pups and to have to distinguish them from their own. On the other hand, fostering behavior may have evolved because it has positive benefits. There are several hypotheses to account for the evolution of fostering behavior: increased maternal experience, continuation of normal reproductive cycle, and increased inclusive fitness (kin selection). Riedman and Le Boeuf (1982) have suggested that some combination of these factors may explain fostering behavior in northern elephant seals (*Mirounga angustirostris*).

Whatever the reason for its evolution, we may be able to use the apparent lack of



Fig. 1: Female Hawaiian monk seal with two pups. One of the pups is not hers but has been temporarily adopted. This represents an unstable situation, because the female will not continue to nurse both pups. The rejected pup will have to be adopted and nursed by another lactating female if it is to survive. The feeding and care of another animal's offspring is called fostering. Photo by M. Craig

own-pup recognition in Hawaiian monk seals to aid in the recovery of this endangered species. A separated, abandoned, or prematurely weaned pup with little chance of survival can, with human assistance, be reunited with a lactating female, who will then nurse it through weaning. Here we describe several such successful rescue efforts and discuss their implications for future conservation work.

Human-assisted Fostering

The breeding range of the Hawaiian monk seal (Fig. 1), one of Hawai'i's two native mammals, is from Nihoa Island to Kure Atoll in the Northwestern Hawaiian Islands. Occasional births occur in the main Hawaiian Islands. Last year they included a birth on Kaua'i and the first recorded birth on O'ahu in modern times. Individual adult females can often be recognized by distinctive scars and natural marks in the pelage, and nicks and cuts on the flippers. Pups are more difficult to distinguish individually because they lack scars. However, pups pass through definite stages (termed P1 through P5 in our field notes) during the nursing period, and, combined

with the fact that the mother-pup pairs usually remain on the same section of beach, it is often possible to follow a pup during its nursing period with reasonable certainty. Weaning occurs after an average nursing period of 39 days (T.C. Johanos, manuscript in prep.) at stage P4 or P5. Similar estimates, based on smaller samples of females, have also been reported (35 days: Kenyon and Rice 1959; 37 days: Johnson and Johnson 1984; 41 days: Boness 1990).

The four cases of successful human-assisted fostering described below took place at French Frigate Shoals, Northwestern Hawaiian Islands. French Frigate Shoals is an atoll composed of about 10 more or less permanent sand islands and one volcanic pinnacle (Amerson 1971). From beach counts of 250-300 seals made during recent years, it is estimated that about half of the current monk seal population lives at this atoll (Gerrodette 1985). East and Whale-Skate Islands are the two most important breeding islands at French Frigate Shoals (Westlake and Gilmartin 1990). Tern Island is an important hauling site, but births rarely occur there. The number of seals using Tern Island has increased greatly over the

last 15 years since the U.S. Coast Guard abandoned a loran station on the island (Schulmeister 1981, Gerrodette and Gilmartin 1990).

Case #1: East Island, 1986

Female B had two P1 pups with her at 1300 hours on 20 April. One pup looked approximately a day older than the other, which still had its umbilical cord attached. Both pups suckled briefly, but were interrupted by the female. She alternately attacked and fled short distances whenever the pups approached. From the water's edge, the female hauled up to the beach crest, traveled in circles, and eventually headed back down to the water. Both pups attempted to follow her, but they moved slowly and appeared to become tired and weak. The smaller pup became stranded at the beach crest. We decided to intervene because of the risk of the pup developing heat stress. At 1504 hours we picked up the extremely hot pup, cooled it in the ocean, and carried it to an adult female that lay nearby. This female vocalized and chased the pup away. Female F was sighted in the water, investigating the shoreline. As soon as she saw the pup, she began giving characteristic "moaning" vocalizations often emitted by mothers to attract pups (Eliason et al. 1990). We placed the pup on the berm, and female F and pup immediately moved toward each other. She nuzzled the pup all over and rested her chin on it. The pup had not suckled, but the pair was asleep, hauled up for the night, when observations ended at 1557 hours. It is unknown whether this pair remained together or if further pup exchanges took place. However, the pup survived to weaning, even though its exact identity was unknown, because all pups on the island at the time weaned.

Case #2: East Island, 1986

On the same day as the previous incident, female H was swimming with one P1 pup when she was approached by another swimming P1 pup about 1600 hours. The female vocalized repeatedly but did not attack either pup. When the trio hauled out, we could see that one pup was slightly larger, and the larger pup blocked the smaller from nursing. Female H was still accompanied by both pups the following day. She appeared agitated whenever the pups attempted to suckle and

neither pup was nursed for a sustained period. Only one pup (usually the larger) was able to get into suckling position at a time. At 1450 hours female M was seen swimming nearby, making the same "moaning" vocalizations described above, and investigating each mother-pup pair along the beach. We decided to intervene because it was unlikely that female H could successfully wean both pups. At 1500 hours we picked up the pup farthest from the sleeping female H (the larger one). The female did not awake. We placed the pup at midbeach in front of searching female M. She immediately hauled out, approached the pup, nosed it, and presented her ventrum. The pup began to suckle three minutes after being placed on the beach, and continued for 15 minutes. The pup soon fell asleep, and the pair was still asleep together when observations ended at 1753 hours. As with Case #1, it is unknown if the pair remained together, but all pups on the island at the time survived to weaning.

Case #3: Whale-Skate Island, 1988

Female W10 was accompanied by both P1 and P2 pups on 24 May. The female alternately repulsed one pup or the other, and neither pup was able to suckle in an hour of observation. The next day a P2 pup (presumably the same one as the previous day) was with female W10; a P1 pup was alone nearby and its movements appeared weak. We knew that female W6 had been nursing a young pup two days previously, but that she had been without a pup since then, so it was likely that she was still lactating. At 1530 hours we picked up the lone pup, carried it 50 m down the beach, and placed it near female W6, who was sleeping at the water's edge. Female W6 did not see us approach but turned and saw us as we were moving away. The adult female and pup both vocalized, moved together, and sniffed each other. About two minutes after the pup was placed near her, the female rolled on her side, presenting her ventrum to the pup. The pup immediately began to suckle. For the next two days, female W6 was seen, apparently with the same young pup, but on 28 May, female W7 appeared to be nursing the pup we had picked up (based on the size of the pup), and female W6 had a larger pup. After that, female W7 continued to be seen every few days with what was probably the same pup

until weaning occurred about 25 June.

Case #4: Tern and Whale-Skate Islands, 1988

An abandoned P1 pup was found on Tern Island on 16 June. From observations the previous day, we knew that female W28 on Whale-Skate Island, 5.5 km away, had become separated from her four day old pup. We did not know if the Tern Island pup belonged to female W28, but we considered it likely. Finding any young pup on Tern Island was a rare event, so finding a separated pup of just the proper size right after female W28 had lost her pup was a highly unlikely coincidence. Moreover, on other occasions we have seen young pups, who are weak swimmers, swept away by currents. Since prevailing winds blow from Whale-Skate toward Tern, W28's pup could have been carried in that direction. We picked up the pup, took it by boat to Whale-Skate Island, and placed it with female W28. She seemed to reject the pup at first, but the next day the pair was nursing normally. The pair continued to be seen together over the next month until the pup weaned about 15 July.

Discussion

Alloparental care (care of young by helpers other than the biological parents) occurs in a wide variety of mammals and birds (Riedman 1982). Such behavior seems to be reproductively costly and unlikely to evolve under classical natural selection. However, there are several possible ways that altruistic behavior such as alloparenting may evolve (Krebs and Davies 1987). By helping raise another's young, a helper may increase its own survival rate, obtain a breeding territory, and gain valuable parenting experience, all of which may contribute to greater production of its own offspring later in life. This appears to be the case among some birds (Emlen 1978) and primates (Lancaster 1971, Hrdy 1976). Riedman and Le Boeuf (1982) suggest that fostering behavior may be beneficial in northern elephant seals by continuing a regular reproductive cycle after losing a pup. This is based on the assumption that lactation and continued nursing help induce ovulation and copulation, and therefore increase the chance of giving birth the next year.

Fostering behavior may also have evolved through kin selection, in which the helpers are related to the young they care for. The theory of kin selection (Hamilton 1964, Michod 1982) postulates that the costs of helping are balanced by the benefits of genetic relatedness. By increasing the probability of survival of relatives, the helpers increase the probability of passing on some of their own genes. However, Boness (1990) did not find any reproductive costs associated with pup exchange behavior in the Hawaiian monk seal. Also, we do not know if Hawaiian monk seal pups involved in pup exchanges are related, or if females tend to foster pups related to them. Genetic studies in progress may allow us to answer some of these questions.

Among pinnipeds, fostering is more common in phocids (true seals) than in otariids (sea lions and fur seals), but most instances have occurred after human disturbance at the pupping colonies (Stirling 1975). In Hawaiian monk seals, an early instance of nursing an alien pup after human disturbance was described by Kenyon and Rice (1959). However, exchange of pups can also occur repeatedly under natural conditions (Boness 1990). Mother-pup recognition seems to involve visual, olfactory, and auditory cues (Eliason et al. 1990), but "mistakes" occur frequently, at least at some locations.

For several years the National Marine Fisheries Service has conducted a successful rehabilitation program for prematurely weaned female monk seal pups at French Frigate Shoals (Gerrodette and Gilmartin 1990). In this rehabilitation program, weaned female pups less than 90 cm in girth are transported to Honolulu for intensive care and feeding, then released as yearlings back into the wild the following spring. However, the weaned pups taken for rehabilitation are much larger than the young pups in the human-assisted fostering cases described above. Rehabilitation of very young pups has not yet been attempted with the Hawaiian monk seal. The remote location makes it difficult and expensive to transport seals, and the chances of successful rehabilitation from such a young age are unknown. Two young Mediterranean monk seal pups (*M. monachus*) were successfully reared in 1988 at the Seal Rehabilitation and Research Centre, Pieterburen, Netherlands, and released into the wild in 1989 (t Hart

and Vedder 1990).

The cases of human-assisted fostering described above offer an alternative to captive rehabilitation that is preferable from several points of view. It is less expensive and involves less handling of the pup. The pup does not risk exposure to exotic diseases which might be carried back into the wild population. Possible long-term effects of hand-rearing in captivity are unknown, but it seems unlikely that removal of an otherwise healthy pup from natural conditions will be better than foster maternal care in the wild, especially when fostering is known to occur naturally.

However, there are stringent requirements that will limit the application of such a procedure. First, abandoned pups must be discovered promptly. Field observations suggest that newborn pups will become too weak to suckle if abandoned for more than a few days. Older pups can survive somewhat longer periods of fasting. Because of intensive field work, we were able to act promptly when the situation arose in these four cases.

Second, successful fostering of an abandoned pup requires the availability and identification of a lactating female without a pup. Unless parturient females have been individually identified and closely followed during the pupping season, it usually will not be known which females are lactating when an abandoned pup is found. In each of the cases above, we either knew that a particular female had recently lost a pup, or saw a female exhibiting a characteristic pup-searching behavior.

Third, there may be other factors affecting successful fostering that we do not understand. An attempted fostering at Laysan Island in 1988 was not successful (Johanos et al. 1990). An attempted reunion of an abandoned pup with a lactating female at East Island in 1983 was not successful (W. G. Gilmartin, pers. comm.). The lack of success in the latter case may have been due to the older stage of the pup (P3), but older pups have also been known to be adopted by lactating females, either with or without their own pup (Alcorn and Henderson 1984, Boness 1990).

Finally, because the Hawaiian monk seal is an endangered species, human intervention during the nursing period is not to be taken lightly. Some of the recent declines in monk seal population size are related to past disturbance at the pupping sites (Gerrodette and Gilmartin 1990).

Moreover, disruption of normal maternal care has been a factor in the decline of many threatened and endangered mammals (Oldfield 1988). In the cases described above, we intervened only when the situation seemed serious, and we attempted to minimize our presence. In all four cases, the adopting female was aware of humans, probably through both sight and smell, but that did not preclude successful fosterings.

Under the right circumstances, therefore, human assisted fostering of abandoned monk seal pups appears to be an effective means of "rescue." To date, alloparental care has been exploited as a conservation strategy mainly in birds, most notably in the case of Sandhill Cranes (*Grus canadensis*) incubating and raising young Whooping Cranes (*G. americana*) (Doughty 1989). The success of the attempts described above suggests that natural fostering behavior could also be exploited as a limited conservation strategy in the Hawaiian monk seal.

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MARINE MAMMAL RESOURCES

PINNIPEDS

History

There are six pinniped species inhabiting the California coast and offshore islands: the California sea lion (*Zalophus californianus*), Steller (or northern) sea lion (*Eumetopias jubatus*), Pacific harbor seal (*Phoca vitulina*), northern elephant seal (*Mirounga angustirostris*), northern fur seal (*Callorhinus ursinus*) and Guadalupe fur seal (*Arctocephalus townsendi*). The ribbon seal (*Phoca fasciata*) and the hooded seal (*Cystophora cristata*) have been reported in California waters, but these were extremely rare events and they are not considered normal California visitors.

The California sea lion and Pacific harbor seal are probably the best known and most often seen pinnipeds in California waters. Californians and visitors from around the world enjoy watching the playful behavior of these animals cavorting in the water near shore or hauled out to rest on buoys, rocks and other solid objects. They also enjoy seeing them in public display aquaria or as performers in animal shows at zoos and parks. Pinnipeds are amusing and intelligent entertainers, but there is another aspect of the pinniped story which is related to their diet of fish and their expanding populations.

In recent years, California sea lions have gained notoriety by taking over portions of marinas in Monterey and San Francisco Bays and by eating endangered or threatened salmon and steelhead moving upstream to spawn. Marina operators and boat owners consider them a major nuisance, but revenue brought by tourists eager to see them has quieted many of their complaints. Some who fish commercially or for sport believe that pinnipeds compete for fish or are costly pests consuming tons of valuable fish, destroying valuable fishing gear and interfering with fishing operations. They complain that any sea lion is attracted to fishing operations and that the mere presence of a sea lion scares fish away from the fishing area. Research biologists speculate that most of those problems are caused by a relatively few "rogue" pinnipeds. Those rogues have learned that a fish caught in a net or hooked on a line is an easier meal than a free-swimming fish. A major concern is that this behavior will spread as the pinniped populations grow.

Faced with decreasing catches, increasing marine mammal populations and increasing fishery interactions, some sport and commercial fishers contend that sea lion populations have reached the point where nuisance animals should be exterminated. On the other hand, environmental groups and marine mammal aficionados support these animals and feel their populations should be allowed to increase unimpeded by human interests or needs.

Food habit studies conclude that pinnipeds consume a variety of prey species, depending on availability, and that, contrary to claims made by many fishers, the normal pinniped diet does not usually include fish which are considered valuable for sport or sale. Their main diet consists of fish such as anchovies, mackerel, herring, hake, rockfish, salmon, and

cephalopods such as squid and octopus. An example of their opportunistic feeding behavior was seen during the 1982-1983 El Niño event. Pelagic red crabs, usually not found in large numbers off California, were very abundant at that time, and were found to be a major diet component for sea lions until ocean conditions returned to normal.

In the 1860's and 1870's, many pinnipeds were killed for their oil or body parts and many females (cows) were captured for displays or animal acts. Pinnipeds were hunted commercially until 1938, when California law gave them complete protection from hunting. Nevertheless, sport and commercial fishers were free to kill sea lions and harbor seals that were destroying gear or otherwise interfering with fishing operations. In 1972, the Marine Mammal Protection Act was passed prohibiting the take (pursuit, harassment, capture, or kill) of marine mammals except under special permitted conditions. Such conditions include research, public display, certain fishery interactions, or entanglement in fishing gear.

To determine the extent of the intentional and accidental kills in various fisheries, observers were placed aboard fishing vessels. Their observations, along with calculations of fishing effort, were used to estimate total numbers of marine mammals killed during fishing operations. In California waters, it was estimated that 2,000 to 4,000 California sea lions, fewer than 100 elephant seals and between 800 and 2,000 harbor seals were killed annually during the 1980-1990 period.

Research has been conducted on methods of reducing the impacts that pinnipeds have on certain fisheries. Taste aversion substances and acoustic harassment devices have been tested but have met with only moderate success. In most cases, the animals appear to acclimate to the deterrents, and sometimes have used the purported scare devices as "dinner bells" signifying active fishing boats and an easy food source.

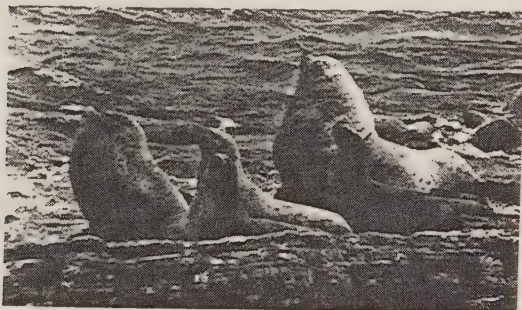
Status of Biological Knowledge



California sea lion, *Zalophus californianus*.

California sea lion. The California sea lion ranges from British Columbia south to Tres Marias Islands off Mexico.

Breeding grounds are mainly on offshore islands from the Channel Islands south into Mexico. Breeding takes place in June and early July within a few days after the females give birth. The pups are weaned at six months to a year or more. Males and females reach sexual maturity between four and five years of age. Males weigh between 500 and 1,000 pounds and reach seven to eight feet in length. Females weigh between 200 and 600 pounds and reach six feet. Adult males have a pronounced sagittal crest (a ridge on top of the skull extending from the forehead to the rear of the skull), a characteristic distinguishing this species from the Steller sea lion. Food of the California sea lion consists largely of squid, octopus, and a variety of fishes (anchovies, mackerel, herring, rockfish, hake, and salmon).



Steller sea lion, *Eumetopias jubatus*.

Steller sea lion. The Steller sea lion's distribution partially overlaps that of the California sea lion. It ranges from the Bering Strait off Alaska to southern California. Breeding grounds extend from the Pribilof Islands to the Channel Islands; however, only a small percentage breeds south of Año Nuevo Island. The largest breeding colonies in California are at Año Nuevo and the Farallon Islands. Breeding is in late June, after which the animals migrate northward. This species is a tawny or yellowish-brown color in contrast to the darker reddish color of the California sea lion. Males are 1,500 to 2,200 pounds and reach a length of 13 feet. Females can weigh a little over 600 pounds and reach a length of nine feet. Food of the Steller sea lion consists primarily of squid and fish. Because of recent declines in the population, Steller sea lions have been designated as threatened under the Endangered Species Act.



Pacific harbor seal, *Phoca vitulina*.

Pacific harbor seal. The Pacific harbor seal ranges along the northwest coast of America from the Gulf of Alaska to

Cedros Island off Baja California. For management purposes, the U.S. harbor seal population has been divided into three stocks as follows: 1) Washington inner coastal waters, 2) Washington and Oregon outer coastal, and 3) California. In California, harbor seals are abundant along the entire coast. Adult male Pacific harbor seals reach a length of six feet and weight of up to 240 pounds, while females reach 5.5 feet and 275 pounds (when pregnant). The coloration patterns of adults vary from black with white spots to white with black spots. Breeding season varies with latitude, starting in April to May on the Channel Islands of southern California and continuing later up the coast. Age at sexual maturity is three to four years for females and five years for males. Newborn pups are approximately 32 inches in length and weigh about 22 pounds. They are weaned at five to six weeks at an average weight of 50 pounds. Adult females ovulate and mate at the end of weaning, with a two-month delayed implantation of the developing embryo. Their diet consists of fish such as flounders, herring, tomcod, hake, and lampreys, and cephalopods such as squid and octopus.



Northern fur seal, *Callorhinus ursinus*.

Northern fur seal. The northern fur seal is one of the best-known seals in the world because of its valuable fur, for which it was hunted to near extinction. Historical populations centered on the Pribilof Islands, Alaska, are estimated at two million animals, but in 1911, when international treaties were established to protect and manage this species, there were fewer than 125,000 animals. San Miguel Island, off Santa Barbara, California, hosts a small breeding colony and is the southernmost extent of its range. The peak breeding and pupping period is in July. After breeding, the males migrate out to sea where they spend as many as 10 months. The pups are weaned at four months of age and are left to travel in the northward migrations on their own. Fur seals are distinguished from sea lions by their pelage, composed of a very dense undercoat and a thinner, coarser layer of guard hairs, and by their relatively long flippers. The northern fur seal is closely related to the Guadalupe fur seal and is distinguished from its close relative by its very short muzzle. Males reach a length of eight feet and weigh up to 700 pounds. Females are only four to five feet in length and weigh about 130 pounds. Sexual maturity is attained between three and seven years of age, with longevity reported to be up to 26 years.



Guadalupe fur seal, *Arctocephalus townsendi*.

Guadalupe fur seal. The Guadalupe fur seal was presumed extinct until 1926, when a group of 60 animals was discovered on Guadalupe Island, Mexico. The population is recovering slowly from near extinction brought about by sealers in the last century. This is a rare pinniped in California waters, seen only occasionally at islands in the Southern California Bight. They breed only on Guadalupe Island and the total population is estimated to be less than 2,500 animals. They are identified by a "collic-like," long pointed muzzle. Males reach up to six feet in length; females are slightly smaller.



Northern elephant seal, *Mirounga angustirostris*.

Northern elephant seal. The comeback of the northern elephant seal, the largest of all the seals, is one of the great success stories for an animal threatened with extinction. Male elephant seals reach a length of 15 to 16 feet and weight of about 4,000 to 5,000 pounds. Females reach a length of 11 feet and weigh about 1,700 pounds. The male develops a bulbous enlargement of the snout from which, along with its size, it gets its common name. Breeding colonies exist on San Miguel Island, Santa Barbara Island, San Nicolas Island, Año Nuevo Island, Southeast Farallon Island, and Point Reyes Peninsula. They have also begun hauling out at several other mainland sites where historically they did not haul out. The breeding season is from December through March. Harems consist of one male and eight to 40 females. The gestation period is about 11.5 months. Pups are weaned by four weeks but remain on the rookery another eight to 10 weeks, sleeping during the day and gradually starting to enter the water at night. Departure from the rookery occurs at an age of approximately three months.

Females begin breeding as young as two years of age. Males reach sexual maturity at five years; but older, larger males prevent young and socially immature males from mating until they are at least eight or nine years old. Males and females both live about 14 years.

Elephant seals do most of their feeding at night and probably in deep water as evidenced by the fact that they have been caught in nets at 2,000-foot depths. Time-depth recorder experiments show that elephant seals can dive to 5,200 feet, and stay beneath the surface for up to an hour. Stomach content analyses indicate that they feed on small sharks, rays, ratfish, rockfish, and squid.

Status of Populations

The Marine Mammal Protection Act recognizes marine mammals as components of the marine ecosystem and requires maintenance of stocks above levels at which they would lose their function in the ecosystem. In practice, marine mammal management is directed toward maintaining the optimum sustainable population size (OSP) for each species within its geographical range. To be optimal, the population size should be between the rate at which maximum growth occurs and the carrying capacity of the environment. A variety of procedures are used to assess population status.

California sea lion. California sea lions breeding on U.S. rookeries are assumed to comprise a single stock. Their status was last assessed in 1986. At that time, there were approximately 17,800 pups counted on U.S. rookeries, representing 21,000 births. That number of births would represent a total U.S. population (stock) size of about 87,000 animals. More recent unpublished data suggest that the population had grown to about 120,000 animals by 1991. The growth rate was assumed to be equal to that observed before the 1983 El Niño event, at which time the California sea lion population in the Southern California Bight was near the lower end of the OSP range.

Steller sea lion. Population estimates for northern sea lions are based on counts of animals hauled-out during the breeding season. A decline of this species is occurring throughout its range, including the Gulf of Alaska and Aleutian Islands, which support 75 percent of the world's population. The current west coast population of northern sea lions is around 68,000 animals, which is less than half of the population level during 1956-1960. The dramatic decline in numbers of Steller sea lion throughout most of its range has prompted its listing as threatened under the Endangered Species Act and depleted under the Marine Mammal Protection Act.

Pacific harbor seal. From aerial census data, the harbor seal population along the California coast appears to be increasing, and concurrently, the number of occupied sites has increased. In 1991, the mainland count was 18,346 seals, and the count for the eight Channel Islands was 4,743 seals, for a minimum population estimate of 23,089 seals in the California stock. This is a minimum population estimate because a substantial fraction of the population is not hauled out during the census.

The 1986 assessment did not confirm that the stock was large enough to fall within the range of OSP, but the counts since 1982 indicate that the rate of growth may be slowing. However,

the occurrence of the 1983-1984 El Niño and the possibility of increased incidental fishing mortality might have affected the population dynamics of this stock. It is likely that the survival and reproduction of harbor seals were altered during the El Niño period and that some of those effects persisted for several years. Additionally, fishing effort in the gill net fishery increased substantially during the 1970-1990 period and the resultant kill of harbor seals undoubtedly altered the population structure. Fishing effort in the gill net fishery is currently declining and should become less of a mortality factor for harbor seals.

Northern fur seal. In 1983, the estimated abundance was about 1.2 million. No significant changes have been documented since that time, although recent counts of Aleutian Island animals decreased. The adult count at San Miguel Island, the only place in California where the northern fur seal breeds, was around 4,000, which was a very small percentage of the worldwide population in 1984. Fur seals are occasionally taken incidentally in the high-seas gillnet fisheries for salmon and squid. They also entangle in discarded fishing debris and die. Although entanglement mortality is not known, there is evidence that it may be contributing to declining trends in the Pribilof Island population. That population has been designated as depleted under the Endangered Species Act and the Marine Mammal Protection Act. Further research on population assessment and trend analysis for the California Channel Island population is needed to determine its size and growth rates.

Guadalupe fur seal. The historical distribution and abundance of the Guadalupe fur seal are unknown because commercial sealers and other observers failed to distinguish between it and the northern fur seal in their records. This species, once thought to be extinct, has an estimated population of about 1,500 to 2,000 animals, with an annual pup production of approximately 200 pups. Although the primary breeding colony is on Guadalupe Island, recent sightings of adult and juvenile seals on some of the Channel Islands suggest that recolonization of that area may occur in the future. The Guadalupe fur seal is listed as threatened under the Endangered Species Act and depleted under the Marine Mammal Protection Act. These listings are based on the concept that the population could become endangered within the foreseeable future, even though it currently does not appear to be in danger of extinction. The population is being closely monitored.

Northern elephant seal. The exploitation and subsequent recovery of the northern elephant seal population is a remarkable story. Biologists estimate that only 100 to 500 animals were left on Guadalupe Island before protective legislation was passed. They claim that the entire current population may have originated from this small group of animals. Based on pup counts, the current U.S. population has grown to an estimated 80,000 animals, ranging from Alaska to Baja California. The apparent growth rate since 1980 has been about 8.75 percent annually. Annual surveys indicate that this species has reoccupied most or all of its historical rookeries and hauling grounds. Using data through 1986, the population appears to be

within the OSP. Presumably, the increased size of the population may lead to increased interactions with fisheries and other human activities.

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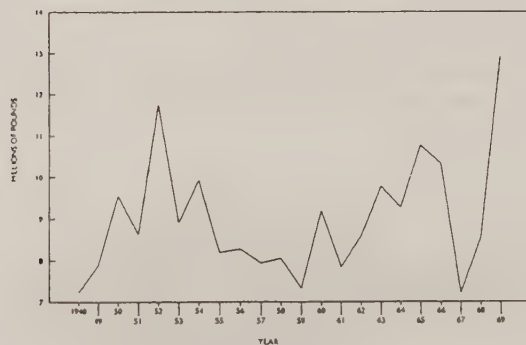
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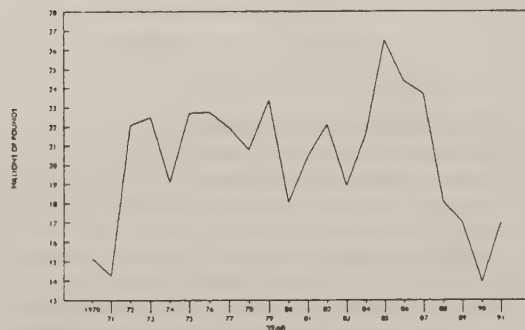
result of market demand during and following World War II and technological advances in fish handling and processing.

At the advent of trawling in the 1870's, Dover sole were inadvertently caught by lateen sailboats using paranzella nets. California's Dover sole fishery expanded from its beginning in San Francisco Bay to its present scope extending from Santa Barbara to the Oregon border. The developing trawl fishery experienced major changes in vessels and netting. Sailboats were replaced by steam, gasoline, then diesel-powered vessels. The original paranzella trawl net was supplanted by the more efficient otter trawl in the 1920's. By the 1980's, some trawl fishermen began to use roller or bobbin trawls to capture Dover sole and other deep-slope groundfish instead of more conventional trawls with rubber mudlines between the trawl doors and footrope to create a fish-herding mud cloud. A quick-freezing method, developed during World War II, hardened the soft flesh of the Dover sole to produce marketable fillets. This advance and the wartime demand for fish allowed trawlers to turn their attention to the large north coast population of Dover sole.

The directed Dover sole fishery began in 1943 when 28 tons were landed. Between 1944 and 1947, landings ranged from 62 tons to 1,400 tons. The fishery expanded to 3,600 tons in 1948, at which time Dover sole landing records were separated from nominal or unspecified sole landings, and rose further to 5,850 tons by 1952. Annual landings then remained stable at approximately 4,000 tons until 1969. From 1969 through 1989, landings have averaged 10,200 tons annually.



California commercial landings of Dover sole, 1948-1969.



California commercial landings of Dover sole, 1970-1991.

DOVER SOLE

History of the Fishery

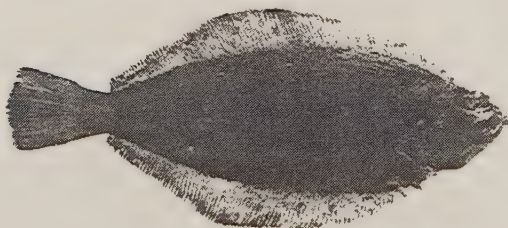
The stature of Dover sole (*Microstomus pacificus*) has evolved from that of an undesirable by-product of bottom trawling prior to the 1940's to become the most abundant groundfish in statewide landings. This phenomenal rise was the

Actual historical catches of Dover sole were undoubtedly higher than reported landings due to at-sea discarding as a result of market-imposed landing limits. Dover sole from deep depths are often "jellied" (have flesh with a high water content) and consequently have reduced market appeal. Because Dover sole are typically captured jointly with other marketable groundfish, especially sablefish and thornyheads, trawling would often continue for co-occurring species, even after landing limits had been reached.

Commercial Dover sole landing limits were imposed coastwide in 1989 and 1990 by the Pacific Fishery Management Council as a trip limit on the aggregate poundage of Dover sole, thornyheads, and sablefish on board. Prior to that time, market demand and gear regulations, not resource availability nor quotas, were the dominant forces controlling statewide Dover sole landings. The intent of this regulation was to reduce the harvest of sablefish by restricting deep water trawl effort for the complex of Dover sole, thornyheads, and sablefish.

The port of Eureka has historically supported the largest Dover sole fishery, followed by Fort Bragg, Crescent City, San Francisco, and Monterey. The Morro Bay-Port San Luis area supported a very minor deep water trawl fishery until 1983 (annual landings of 50 tons), at which time a wintertime influx of trawlers from northern California and Oregon began targeting Dover sole. Good winter weather, an absence of market limits, and a relatively unexploited resource caused landings to rise dramatically. From 1983 to 1989, landings into Morro Bay and Port San Luis have averaged 1,760 tons.

Sport utilization of Dover sole is practically nonexistent. The depth distribution of Dover sole normally places them beyond most sport fishing activity, and Dover sole, because of their feeding habits, are not vulnerable to hook-and-line fishing.



Dover sole, *Microstomus pacificus*.

Status of Biological Knowledge

Dover sole occur from the Bering Sea to northern Baja California on mud bottoms at depths from 180 to 4,800 feet. Although early tagging experiments off Oregon and California suggested Dover sole move inshore in the summer, a more recent California Department of Fish and Game (CDFG) tagging study discovered that not all Dover sole participate in the summer inshore movement. In fact, most of the mature fish tagged and released in deep water were recovered in deep water regardless of season. Thus the CDFG tagging data indicate that two substocks may exist: one that migrates and one that does

not. Juvenile Dover sole settle on the continental shelf and gradually move down the slope over their lifetime, reaching the oxygen-minimum zone as they become sexually mature. Thus, fish composing the migratory substock may be younger than those composing the nonmigratory substock.

Fish size changes markedly with ocean depth. For example, the average weight of females increases from 0.61 pound in depths shallower than 1,500 feet, to 1.80 pounds in 1,500 to 3,300 feet, then to 2.46 pounds from 3,300 to 4,200 feet. The proportion of females also increases with depth, from two-thirds of the total biomass in shallow waters to over 90 percent at depths greater than 3300 feet.

Growth is rapid during the early years of life but decreases with age. Five-year-old Dover sole grow 0.65 inch per year, but, by 10 years of age, growth slows to 0.42 inch annually. Dover sole may attain an age of over 50 years and reach 30 inches in length. Fifty percent of Dover sole females 12.2 inches long are mature. The smallest mature Dover sole in 1987-1988 studies was six years old, whereas early studies reported mature five-year-old females.

Dover sole may spawn nine batches to release all eggs in a spawning season. Egg production is correlated with size. Fish of 0.55 pound produce 33,000 eggs, while 2.36-pound fish produce 54,000 eggs on average. The buoyant Dover sole eggs may experience a wide range of water temperatures, from 37 degrees F near the bottom to 59 degrees F at the sea surface. Thus, incubation time may vary from 10 days to one month. Larvae have a prolonged pelagic life of at least one year and are unusually large (one to two inches long) before settling to the bottom. Larvae have been found along the entire California coast, as far as 60 miles south of the U.S.-Mexico border and up to 280 miles offshore.

Dover sole feed commonly on polychaete worms, pelecypod and scaphopod mollusks, shrimp, and brittle stars. Only Pacific sleeper sharks and spiny dogfish are known to prey on Dover sole.

Status of Population

Population estimates of Dover sole in California waters are only available for limited geographic areas in central and northern California. In 1987 and 1988, the National Marine Fisheries Service (NMFS) conducted two surveys to assess the adult biomass of Dover sole in the area from Point Conception to Monterey Bay. The surveys found that 98 percent of the spawning biomass of Dover sole in central California waters live on the continental slope between 2,100 and 3,300 feet deep, an area characterized by low oxygen concentrations and very cold temperatures. Estimated biomass was 11,250 tons using one survey method and ranged from 15,400 to 18,700 tons using the other.

A Dover sole stock assessment using 1990 NMFS bottom trawl survey data and population modelling provided estimates of current biomass and yields for the area from Cape Mendocino, California to Cape Blanco, Oregon. Female spawning biomass was estimated to be 20,200 tons, with a likely range of 16,500 to 34,000 tons. Estimated maximum sustain-

able yield for the Eureka area is 3,000 to 4,100 tons. The stock in this area was in equilibrium and near the target biomass level that would provide maximum sustainable yield.

A quantitative assessment has not been conducted yet on the Dover sole population in central California between Monterey Bay and Cape Mendocino.

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LETTERS TO NATURE

Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*)

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TUNA are unique among teleost fishes in being thermoconserving. Vascular counter-current heat exchangers maintain body temperatures above ambient water temperature, thereby improving locomotor muscle efficiency, especially at burst speeds and when pursuing prey below the thermocline¹⁻⁶. Because tuna also occasionally swim rapidly in warm surface waters, it has been hypothesized that tuna thermoregulate to accommodate changing activity levels or ambient temperatures⁷. But previous field experiments have been unable to demonstrate definitively short-latency, mammalian-type physiological thermoregulation^{8,9}. Here we show using telemetered data that free-ranging bigeye tuna (*Thunnus obesus*) can rapidly alter whole-body thermal conductivity by two orders of magnitude. The heat exchangers are disengaged to allow rapid warming as the tuna ascend from cold water into warmer surface waters, and are reactivated to conserve heat when they return into the depths. Combining physiological and behavioural thermoregulation expands the foraging space of bigeye tuna into otherwise prohibitively cold, deep water.

In all fish, oxygenated arterial blood leaves the gills essentially equilibrated to ambient water temperature (T_a). But in tunas, arterial blood passes through dense retia of interdigitated veins carrying warm blood away from the swimming muscles. The whole-body heat-transfer coefficient (k) is thereby reduced and heat is returned into the tissues¹⁻³. Although elevated body

temperature (T_b) improves locomotor muscle power for these obligate swimmers when they are at high speeds or below the thermocline^{4,5}, a permanently engaged heat retention system could be counterproductive for tuna swimming rapidly (fleeing, or chasing prey) in warm surface waters, because T_b may rise to injurious levels. Thus, it has been postulated that tuna can modify thermoconservation efficiency to fit the immediate demands of activity level and thermal environment⁷.

Studies with captive tuna have been suggestive of an ability to regulate k by a few per cent (probably through altered cardiac output which changes the dwell time of blood in the retia)^{7,10}, but data from field experiments with bluefin tuna (*T. thynnus*), are ambiguous^{8,9}, and a transmitter placed in a bigeye tuna stomach failed to demonstrate thermoregulation⁸. Hysteresis in the warming and cooling rates of swordfish, *Xiphias gladius*, occurs over periods of hours¹¹ and is associated with irregular diving patterns, making it difficult to separate the effects of changes in activity level, cardiac output and thermal inertia imparted by simple heat exchangers^{3,11-13}. Tuna, however, experience very rapid changes in T_a , which would require fast thermoregulatory adjustments. Thus, the question remained: can tuna perform physiological thermoregulation, or are the retia simply passive devices sensitive to blood flow rate?

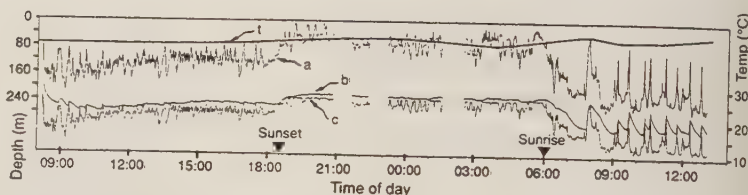
The behaviour of subadult bigeye tuna in Hawaiian waters is ideal for testing for the occurrence of physiological thermoregulation. During daytime, they select temperatures between 14 and 17 °C (at depths around 250 m), from which they make regular periodic, rapid vertical excursions up into warmer waters¹⁴. During these excursions, the fish experience first increasing and then decreasing T_a , changing at up to 12 °C min⁻¹. The comparatively small size of these tuna (65 to 80 cm; 7.0 to 12 kg), reduces the influence of simple thermal inertia on T_b .

In open-ocean tracking experiments, we telemetered swimming depth and T_b data from two bigeye tuna, one of which exhibited typical bigeye distribution and behaviour (Fig. 1). The radically different rates of body warming and cooling observed during the vertical excursions were modelled with a numerical parameter estimation procedure¹⁵ which minimizes the squared differences between observed and estimated T_b .

Tuna body temperature is a function of heat exchange with

FIG. 1 Simultaneous swimming depth (a; left axis), T_b (b; right axis) and T_a (c; right axis) of bigeye tuna number 2 (length, 79 cm; weight ~11.7 kg). Acoustic telemetry techniques¹⁸ were used to monitor simultaneously swimming depth and T_b of a free-ranging bigeye tuna for 29 h. T_a was measured by a thermister in the tip of a 6.0 × 0.25 cm hypodermic needle inserted from the dorsal surface. Thermister probe length was pre-set to reach swimming muscles 2 to 3 cm

from dorso-lateral to the spine; angling the probe caudally prevented it from moving during swimming (as confirmed with captive fish). T_a was derived by interpolating between sequential expendable bathythermograph deployments and knowing the depth of the fish. T_b and depth data were recorded on tape on the tracking vessel. This fish demonstrated the typical diel pattern of swimming closer to the surface at night and, on the second



morning, the deep distribution and vertical excursions regularly observed in previous bigeye tracks¹⁴. T_b were buffered against changes in T_a resulting from brief movements up and down through the water column. Solid horizontal line (t) represents the interface between the bottom of the surface mixed layer and the top of the thermocline.

the environment and internal (metabolic) heat production ($\dot{T}_m$). In this case, the symmetry of the rates of ascent and descent, combined with constant horizontal speed over ground, indicated that locomotor output, and hence $\dot{T}_m$, was constant during the observed periods of warming and cooling. Heat loss (or gain) is proportional to the difference between body temperature and the surrounding water:

$$\frac{dT_b}{dt} = k(T_a - T_b) + \dot{T}_m \quad (1)$$

The estimated values of k for warming and cooling which

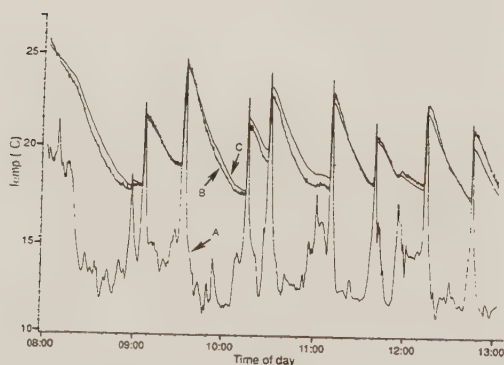


FIG. 2 Relationship between ambient temperature (A), observed body temperature (B), and estimated body temperature (C) for fish number 2, day 2. Using equation (1), and a switching function (equation (2)), automatic differentiation^{15,16} was used to fit two possible values of k to the observed data from fish 2

$$k = \begin{cases} k_1, & \text{if } T_a - T_b \leq \Delta T_{crit} \\ k_2, & \text{if } T_a - T_b > \Delta T_{crit} \end{cases} \quad (2)$$

where k_1 and k_2 are different values for whole-body heat-transfer coefficient such that $k_1 \ll k_2$, and $k = k_1$ when the fish is in heat-retention mode and $k = k_2$ when in heat-absorption mode. ΔT_{crit} is some threshold value for the difference between T_b and T_a , such that the heat exchanger is engaged when the fish is in water that is ΔT_{crit} cooler than T_b and disengaged when in water that is ΔT_{crit} degrees warmer than T_b . The model parameters were estimated in a stepwise fashion: first $\dot{T}_m$, then k_1 and k_2 and finally ΔT_{crit} . Improvement in fit at each step was tested using a simple F test on the decrease in the residual sum of squares. The T_b curves resulting from the modelled k_1 and k_2 values closely match the rapid warming and slow cooling observed during the vertical excursions. These excursions were consistently initiated when T_b declined to ~17.5 °C, possibly indicating a minimum tolerable T_b , even though still 6 °C above T_a . The estimated value for $\dot{T}_m$ was 1.12×10^{-4} °C s⁻¹ and estimated value of ΔT_{crit} was 0.03 °C, within the range of temperature detection thresholds observed experimentally with captive fish^{20,21}.

best fit the observed data (Fig. 2) are: $k_1 = 5.22 \times 10^{-4}$ (cooling), and $k_2 = 4.01 \times 10^{-2}$ (warming). These values indicate that the fish was rapidly varying the rate of instantaneous heat transfer by over two orders of magnitude. Examination of the onset of changes in T_b indicates that the conductivity switches were implemented in about 45 s.

The tunas have progressively evolved away from the typical teleost vasculature; blood supplying the swimming muscles is delivered and retrieved less through central blood vessels running through the haemal arch, and more through sub-dermal retia and cutaneous arteries and veins^{1-3,5}. In the comparatively primitive skipjack tuna (*Katsuwonus pelamis*), there are both central and lateral heat exchangers, whereas the most highly evolved (and most temperate in distribution) bluefin tuna no longer has a complete central blood supply to the musculature, but a complex lateral rete system. This progressive lateralization of blood supply may be a response to the radiation of tuna away from tropical environments; supplying the muscles entirely through lateral heat exchangers most effectively insulates the fish and limits the flow of cold arterial blood into the core⁵.

Bigeye tuna are intermediate in both their vascular design and distribution; they have well developed lateral heat exchangers, and retain a modest central blood supply, but it does not pass through a countercurrent rete^{2,5}. Routing arterial blood through the lateral rete system would put the tuna into a thermoconserving mode (k_1); passing the blood through the central system would result in an essentially poikilothermic fish (k_2). The latency of onset of warming is consistent with adrenergic neural control of vascular dilation¹⁶; in skipjack tuna at least, heat exchanger arteries have smooth muscle in their walls¹⁷.

Although inhabiting semitropical latitudes, bigeye tuna have expanded their range by invading the cooler depths below the surface mixed layer and evolving a behavioural repertoire and circulatory system that take advantage of the vertical proximity of warm water. Their vascular anatomy provides a capacity for short-latency physiological thermoregulation which, when coupled with behavioural thermoregulation expressed as the brief vertical excursions, allows them to forage in deep waters and still maintain the advantages of high muscle temperatures derived from their tropical lineage. □

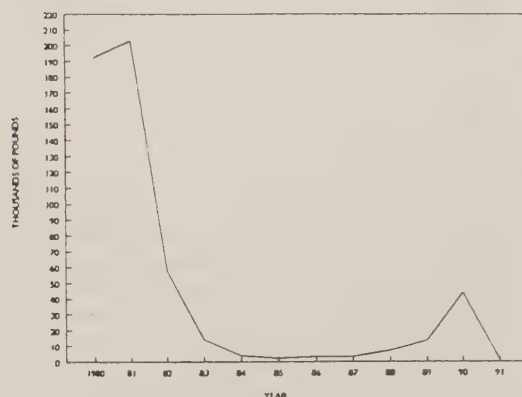
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boats from two to seven nights per week. Catches average 10 to 40 blue sharks per trip, although this varies throughout year.



Commercial landings of blue shark, 1980-91.

BLUE SHARK

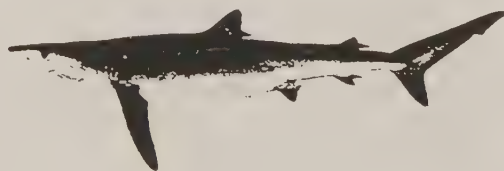
History of the Fishery

Until recently blue sharks (*Prionace glauca*) were not a major target of California's recreational or commercial fisheries. Urea stored in their blood system quickly turns to ammonia when the shark dies, thus rendering the meat unpalatable. Development of a quality meat product has been the limiting factor in creating commercial interest. Only two serious attempts at developing a quality food product in California have occurred. The first took place in 1979 and 1980 when one vessel fished blue sharks experimentally with longline gear. Product quality was judged to be good enough to establish blue shark as a viable alternate fishery, and 150,000 pounds dressed meat were sold at about \$0.25 per pound. Although market interest developed in several western states, a steady demand could not be assured and the fishery was discontinued.

The second attempt at developing a food product began in 1988 with an experimental longline fishery directed at shortfin mako (*Isurus oxyrinchus*) and blue shark. Participants in the fishery were required to develop a market for human consumption with the bycatch of blue sharks which were not released alive. In 1989 and 1990, a total of 54,000 pounds of blue shark was sold for making jerky and "fish and chips." It was clear from these attempts however that a quality food product and related market had not been achieved. Participants in the fishery substantially reduced the incidental mortality of blue sharks by developing a hook removal tool which allowed up to 88 percent of the blue shark catch to be released unharmed. As a result, the requirement to develop a wholesale market for blue sharks was dropped in 1991.

The recreational catch of blue sharks has grown tremendously in recent years. Estimated annual catch increased 10-fold between 1981 and 1988 with over 400,000 angler-trips on private boats which had "sharks" (including mako sharks) as the primary or secondary target species. Most southern California sport fishing areas offer shark fishing trips aboard charter

The greatest source of fishing mortality for southern California blue sharks over the past two decades probably occurred as a result of their incidental capture during the developing years of the drift gill net fishery for swordfish and thresher sharks. Annual estimated bycatch in the late 1970's and early 1980's was between 15,000 and 20,000 blue sharks. Changes in season length, fleet size, time-area closures and the use of large mesh nets substantially reduced blue shark mortality, although there are no reported estimates of current mortality in this fishery.



Blue shark, *Prionace glauca*.

Status of Biological Knowledge

The blue shark is circumglobal in tropical and temperate waters. It is epipelagic and generally considered abundant in the coastal and offshore waters of the western United States and Mexico. In the north Pacific, seasonal migrations occur between 20° and 50° N latitude. The northward movement extends into the Gulf of Alaska as waters warm in the summer months, reversing southward during winter. A seasonal segregation by sex may be influenced by water temperature. Mature females tend to start their northward journey as warmer water moves northward while juveniles of both sexes follow close behind. Large males start later and tend to stay further offshore.

Blue sharks are viviparous. As such, developing embryos are nourished initially from a yolk sac. Once the yolk sac is exhausted, developing young obtain nourishment and oxygen from the maternal blood stream through a placenta. Blue sharks

are released fully formed and independent at birth. Gestation is nine to 12 months. Brood size varies considerably depending on the females size and condition, with over 100 young in a single brood reported, although 20 to 40 young are more typical. Off California, mating occurs in late spring to early winter. The Southern California Bight (SCB) is a major birthing area and is generally considered a nursery area for immature blue sharks, where they are often seen cruising slowly with their dorsal fin and dorsal tail lobe sticking out of the water. Females mature at five to six years and males mature a year earlier. Maximum age is estimated to be at least 20 years.

Blue sharks feed opportunistically on small pelagic fishes including jack mackerel, northern anchovy, Pacific herring, market squid, and red crab. Juveniles make shoreward movements at night to feed in shallow water especially in the SCB, where numerous islands and submerged banks provide ample prey. They also feed on marine mammal carrion but are not known to attack healthy individuals.

Status of Population

The size of California's blue shark stock is unknown. Local abundance undergoes major seasonal fluctuations with juveniles to three year-olds most abundant in the coastal waters from early spring to early winter. Mature adults are uncommon in coastal waters.

Fishery-dependent data needed for determining abundance, mortality, etc. are lacking because blue sharks are usually discarded at sea and the catch often goes undocumented. Local abundance depends on recruitment of juveniles and immigration of individuals from Mexico and offshore into California waters. Although there are no abundance estimates (local or Pacific-wide), some fishermen and field biologists speculate that there are fewer blue sharks than there were 10 years ago. The combined mortality from recreational anglers, commercial set net and drift net fisheries, Mexican fisheries and foreign high-seas fisheries undoubtedly has the potential to impact the population and the local blue shark stock to an unknown extent.

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SHARKS, SKATES AND RAYS: DISCUSSION

Over the past two decades a tremendous amount of fishing pressure has focused on elasmobranchs. Reported catches world-wide exceed 600,000 tons annually. Just 15 years ago sharks, skates and rays were considered one of California's most underutilized resources. But commercial and recreational fisheries targeting California's elasmobranch resources have experienced dramatic growth during this short period, and the growth has made a significant impact on portions of that resource.

The value of these fisheries grew in response to public acceptance of shark as a wholesome and enjoyable alternative to traditional meat products. Led by landings of the common thresher shark in the early 1980's, California's elasmobranch fisheries peaked in 1981 and 1982 at over four million pounds. Landings continued high into the late-1980's, led by the Pacific angel and shortfin mako shark fisheries. The value of shark meat (ex-vessel price) averaged a dollar, or more, per pound for most species throughout this period. Common uses of shark products other than for human consumption include fins, skin, teeth, squalene, liver oil and medical products. The fins, while taken extensively on the east coast for oriental markets, have not developed into a sizeable market in California.

The importance of shark fishing to recreational anglers has also grown rapidly in recent years. Shark fishing trips for shortfin mako and blue sharks on charter vessels are available nightly throughout southern California. Shark derbies have become increasingly popular and angler effort directed at sharks and skates is estimated at a half a million trips annually.

Sharks, skates and rays have existed and adapted to their environment for over 400 million years. Generally, the pelagic species evolved into apex predators while inshore and bottom-dwelling species either approximated apex status or, like the pelagic species, had few natural predators. Elasmobranch reproductive strategy is simple but efficient. They produce a few well developed, strong individuals whose survival is assured because of their advanced development. All elasmobranchs have a slow growth rate, mature relatively late (30-50% of their life span), have a long gestation period or lay large, slowly maturing egg cases. Brood sizes are generally small. Annual production averages two to eight for ovoviviparous species, 20 to 40 for viviparous and perhaps a hundred or more egg cases in the oviparous species.

While this reproductive strategy has served them well in the past, it makes them quite vulnerable to modern day commercial and recreational fishing pressure. Clearly in a population where each mature female produces only a small number of young in each breeding cycle, recruitment is highly dependent on the number of mature females in that population. As Holden pointed out in the mid-1970's, success in establishing a sustained fishery on such a resource is dependent on maintaining a large population of mature individuals. This has not been the case in most fisheries targeting California's sharks. While many of these pelagic species may be found Pacific- or even world-wide, local stocks have experienced a high degree of exploitation. The Southern California Bight (SCB) is, at least in part, a nursery area for several species including the common

thresher, shortfin mako and blue sharks. Nearly all sharks taken within this area are immature. Removing a large segment of juveniles from the population may create a reduced adult population in later years when those exploited juveniles would have become adults and begun reproducing themselves. The ability of local stocks to recover from over-exploitation depends not only on reducing fishing effort, but also on the size of the virgin stock, natural mortality, and migration rates. Also important to certain skates, rays and shallow water sharks is preserving breeding habitat and water quality.

We have learned much about biology and stock structure of many of California's elasmobranch species but there are still no stock size estimates available. Species distributions are poorly understood or known only from fishery dependent data. Many species have contiguous distributions into Mexican and adjacent state waters where they are also subject to fisheries. We have seen much variability in the apparent abundance of shortfin mako, blue, pelagic and bigeye threshers; still others like the Pacific angel and common thresher show a steady decline in apparent abundance. There is no direct evidence that skates and rays have experienced abundance declines, but if a major fishery were to develop or a loss of nursery habitat were to occur through coastal development, pollution, or increased recreational use, they, too, might suffer.

Specific Management Recommendations

Management of California's elasmobranch resources should be a high priority task for fishery managers in the 1990's. This stewardship will not be an easy task. Regulations enacted by special interest groups to benefit only one segment of the resource, combined with the lack of biological information, can only slow progress toward achieving rational management for sustained harvests. Coast-wide and stock-wide data gathering agreements are necessary for stock assessments. Only through decisive action by fishery managers and through public education can these resources be maintained at healthy levels.

Specific recommendations include:

- 1) Develop a coast-wide fishery management regime that recognizes and address the low reproductive capacity of California's elasmobranchs. A major objective is to develop a coast-wide management plan to prevent over-fishing and wastage, while maintaining healthy stocks. This is especially important for the common thresher, shortfin mako, blue, leopard and Pacific angel sharks. A conservative approach is recommended where actual species-specific fishery and biological data are lacking.
- 2) Continue to monitor current fisheries through skipper logs, landing receipts and port samplers with increased emphasis on coverage rates and data quality. On-board observers should be employed when appropriate.
- 3) Initiate a special monitoring or reporting system for shark derbies and on commercial passenger vessel trips targeting mako and blue sharks.
- 4) Begin efforts immediately to conduct a cooperative California-Mexico assessment of transboundary shark populations, including the collection of data from Mexico's Pacific shark fisheries.

5) Develop educational programs to elevate the public's perception of sharks and to promote a conservation attitude towards them.

6) Expand existing CDFG tagging programs to provide critically lacking life history information. This should include taking advantage of tagging opportunities provided by shark derbies, and aboard party boats, private anglers and commercial shark vessels.

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KELP GREENLING

History of the Fishery

Kelp greenling (*Hexagrammos decagrammus*) are fished primarily for sport, but there is a small commercial fishery based largely on catch incidental to the lingcod or inshore rockfish fisheries. Because of their abundance in nearshore rocky areas, they are frequently caught by people fishing from shore or small boats and are a common target for spear fishermen underwater. Sport fishing surveys made from 1958 to

1961 showed that kelp greenling were the most frequent catch of shore fishermen north of San Francisco, where in some areas they made up more than 30 percent of the total catch. In each of those years in California, an average of 54,000 kelp greenling were caught by hook-and-line fishermen and another 2,000 by spear fishermen. In later surveys from 1979 to 1986, the estimated sport catch averaged 116,000 fish per year, with 109,000 of these taken between Monterey County and the Oregon border. It should be noted that the two sport fishing surveys used different sampling designs, and so results may not be comparable. By comparison, the commercial catch reported from 1987 to 1989 averaged about 5,000 fish per year. Most of these were sold in the fresh-fish market. Though filets from kelp greenling are not as large as those from their more popular relative the lingcod, texture and taste are comparable.



Kelp greenling, *Hexagrammos decagrammus*.

Status of Biological Knowledge

Kelp greenling range from San Diego to the Aleutian Islands, but are common only north of Morro Bay. Here they are one of the most conspicuous fishes in rocky nearshore habitats often in and around kelp beds. The male and female look so different that they were first described as separate species. The body color is variable in both sexes, ranging from light gray to brown. Males, however, have large irregular blue patches anteriorly, while females are uniformly covered with smaller dark spots.

These solitary fish are common at depths between 10 and 60 feet, and range down to 150 feet. Sport catches indicate that larger fish live in deeper water. For example, fish caught at 80 to 100 feet range from 12 to 18 inches long while those caught at 20 to 40 feet tend to be eight to 13 inches long. Kelp greenling grow faster than most nearshore fishes during their first three years. After the third year, growth slows, especially in males (as it does in lingcod), so that by the fifth or sixth year males are smaller than females. The maximum reported age and size is 16 years and 21 inches. At age 3, males average 10.6 inches and females 9.1 inches. By age 5, the males average 12.6 inches while females are 14.7 inches. Ten year olds average 15.5 and 16.4 inches, respectively. These studies were done in Puget Sound, Washington.

The reproductive behavior of greenling is similar to that of the lingcod. Females are mature by their fourth year and spawn adhesive egg masses on the seabed and encrusting biota within the territories of courting males. In Puget Sound, females deposit egg masses that range from golf-ball to tennis-ball size, with an average of about 4,000 eggs per cluster. Males fertilize

the eggs and guard them until larvae about one third of an inch long emerge four to five weeks later. Often, males guard more than one egg mass at a time, each possibly produced by a different female. Hatching occurs from December through February in northern California and gets progressively earlier to the north, November through January in Puget Sound and August through September in Alaska. Larvae and early juveniles feed on small copepods and spend about one year in the pelagic environment before entering the nearshore benthic community.

After they settle in the nearshore environment, kelp greenling have flexible food habits. During most of the year, they consume a variety of prey that is consistently available in the habitat, including crabs, amphipods, polychaetes and ascidians. There are brief periods when organisms such as juvenile fishes or herring spawn become exceptionally abundant, and kelp greenling shift their food habits to take advantage of these opportunities.

The primary predators of adult greenling are lingcod, and the harbor seal. As juveniles they probably are prey of many nearshore predators.

Status of Population

There are no estimates of abundance for kelp greenling in California. The yearly sport catch remained relatively constant during the eight years (1979-1986) it was surveyed. Since decline in catch is one symptom of overfishing, there is no indication that current levels of fishing are having adverse effects on the population. Spear fishermen may overfish local populations, however, because they can select individual targets, and greenling are particularly vulnerable to spears when guarding their nests. Other data that could reveal changes in the population structure are not available.

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Abstract.—The potential annual fecundity of Dover sole becomes fixed before the spawning season when the average diameter of the advanced stock of yolked oocytes exceeds 0.86 mm; hence potential annual fecundity is determinate. More central California females had atretic advanced oocytes than Oregon females, but rates of atresia were not sufficiently high to have an important effect on the potential annual fecundity of the population. A 1-kg female matured about 83,000 advanced yolked oocytes at the beginning of the season. Vitellogenesis continued for the advanced yolked oocytes during most of the spawning season while batches were repetitively matured and spawned. About nine batches were spawned over a six-month spawning season (December–May), and spawning ceased when the standing stock of advanced oocytes was exhausted. A 1-kg female released about 10,000 eggs per spawning, except for the first and last batches which were smaller than the rest. Near the end of the season, females may spawn more frequently than earlier in the year, increasing the daily production of eggs by the population even though fewer females are reproductively active. Annual reproductive effort of Dover sole was equivalent to about 14% of body wet weight per year. Fifty percent of the females had become sexually mature when they reached 332 mm total length.

Various methodological issues were also treated in this paper, including validation of key assumptions underlying estimates of annual fecundity; fecundity sample-size requirements; evaluation of criteria and bias in estimating female sexual maturity; and comparisons of classification by histology and gross anatomy.

Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision

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Fecundity and sexual maturity estimates are staples of fishery science. Inevitably, they will be estimated for every species of economic consequence because of their importance in the dynamics of the population. A second reason for studying fecundity is that when fecundity estimates are combined with estimates of the abundance of eggs in the sea, they can be used to estimate the biomass of a stock. Our laboratory is currently evaluating such ichthyoplankton methods for estimating the biomass of Dover sole *Microstomus pacificus*, a large demersal resource occurring along the upper continental slope of the west coast of North America. The fecundity of Dover sole from Oregon has been estimated (Yoklavich and Pikitch 1989), but no estimate exists for the segment of the stock living in central California waters, nor have the assumptions underlying fecundity and sexual maturity assessments been studied with the thoroughness necessary for accurate estimates of adult biomass. Thorough analysis of these assumptions is usually lacking in the fecundity literature.

Our objectives were to describe the reproduction of Dover sole off central California and Oregon, and evaluate the assumptions underlying fecundity and sexual maturity estimates.

We describe changes in the reproductive state of female Dover sole during the spawning season, estimate annual fecundity, batch fecundity, rates of atresia, annual rates of spawning, and length at 50% mature (ML_{50}).

Evaluation of the assumptions underlying annual fecundity estimates requires defining six fecundity terms, and those underlying maturity estimates require defining four terms for reproductive state.

Fecundity

Annual fecundity Total number of eggs spawned by a female per year.

Total fecundity Standing stock of advanced yolked oocytes.

Potential annual fecundity Total advanced yolked oocytes matured per year, uncorrected for atretic losses. In species with determinate fecundity, potential annual fecundity is considered to be equivalent to the total fecundity prior to the onset of spawning.

Determinate fecundity Annual fecundity is determinate when the potential annual fecundity becomes fixed prior to the onset of spawning. In fishes with determinate fecundity, total fecundity decreases with each

spawning because the standing stock of advanced yolked oocytes is not replaced during the spawning season.

Indeterminate annual fecundity Annual fecundity is indeterminate when the potential annual fecundity of a female is not fixed prior to the onset of spawning and unyielded oocytes continue to be matured and spawned during the spawning season.

Batch fecundity Number of hydrated oocytes released in one spawning; usually determined by counting the number of hydrated oocytes in the ovary.

Relative fecundity Fecundity divided by female weight.

Reproductive states

Active Females capable of spawning at the time of capture or in the near future (by the end of the survey or of a season, or other temporal end point). Ovaries of active females contain sufficient number of yolked oocytes for a spawning.

Inactive Females not capable of spawning at the time of capture nor in the near future, although some may have been mature in the past.

Mature Females that have spawned in the current reproductive season or can be expected to do so.

Immature Females that have not spawned in the current reproductive season nor can be expected to do so.

The central methodological issue in fishes with determinate fecundity (Hunter and Macewicz 1985a, Horwood and Greer Walker 1990) is to establish that potential annual fecundity is an unbiased estimate of annual fecundity. For this to be true in Dover sole requires four key assumptions. The first and most important assumption is that fecundity is determinate in Dover sole. This means that potential annual fecundity becomes fixed before spawning begins. Estimation of the standing stock of advanced oocytes (total fecundity) is meaningless if, during the spawning season, oocytes are added to that stock.

The second assumption is that the potential annual fecundity is equivalent to annual fecundity. Strictly speaking, this probably never happens because in any fish population some of the females resorb some of their advanced yolked oocytes rather than spawn them, a process known as atresia. If many females resorbed many of their advanced oocytes, potential annual fecundity would be a serious overestimate of annual fecundity in the population. In addition, not all ovulated oocytes are spawned; a few remain in the ovigerous folds of the ovary after spawning and are later re-

sorbed. Retention of ovulated oocytes is probably seldom a serious bias.

The third assumption is that the females used to estimate potential annual fecundity have not spawned during the current reproductive season. Dover sole females that have spawned some of their stock of advanced oocytes cannot always be distinguished from those that have not begun spawning. Inclusion of partially spawned females in an estimate of potential annual fecundity of the population could be a significant bias.

The fourth assumption is that one is able to identify with certainty the oocytes that constitute the potential annual fecundity. An ovary may not be sufficiently developed to identify all of the oocytes destined to be spawned. On the other hand, if the ovary is highly advanced, spawning may have begun and some advanced oocytes lost. Clearly, an optimal range of ovarian development exists where these risks are minimized.

In addition to evaluating the above four assumptions (determinate fecundity, atresia, spawning, and immaturity) we consider several other methodological issues related to assessment of fecundity and female sexual maturity. These issues are (1) validation of our gross anatomical and histological classification of ovaries into active or inactive and mature or immature states; (2) four precision issues related to total fecundity estimates (number of tissue samples per ovary, number of females, location of ovarian tissue samples, and within-trawl and between-trawl variance); and (3) an evaluation of bias in the assessment of female sexual maturity.

Methods

Collections and shipboard measurements

Dover sole were collected along the central California coast (Point Conception to San Francisco Bay) during six research trawl cruises (Table 1). Dover sole were taken off the Oregon coast between Cape Lookout and Heceta Head during two cruises in 1988-89; miscellaneous collections provided by E. Pritchard off the Oregon coast in 1985 and 1986 were also used. Research trawls were one-half hour or one hour long, depending on depth. In central California waters, we used a 400-mesh Eastern trawl (mouth opening ~15 m wide and 1.5 m high; Watne 1977). In Oregon waters, either an Alaska Fisheries Science Center (AFSC) modified 5-inch mesh, 90/120, high-rise "poly Nor'Eastern" trawl (fishing dimensions ~4.6 m high and 13.5 m wide at wing tips), a 5-inch mesh, 92/83, poly Nor'Eastern trawl, or a 5½-inch mesh, 75/90, high-rise Aberdeen trawl was used. Up to 100 Dover sole from

Table 1

Sources of reproductive data on female Dover sole *Microstomus pacificus*. Number of specimens in three levels of ovarian analysis and number of level-3 females with batch fecundity estimates.

Sampling protocol				Levels of ovarian analysis**				Batch fecundity
Date (Begin/End)	State	No. positive trawl collections	Selection of females*	1	2	3	Total	
				----- (no. females) -----				
3 Dec 85								
12 Dec 85	CA	11	A	—	39	65	104	—
4 Nov 85								
14 Dec 85	OR	4	Unknown	—	73	—	73	—
6 Feb 86								
7 Feb 86	OR	3	Unknown	—	37	—	37	—
3 May 86	OR	2	Unknown	—	27	—	34	7
5 Mar 86								
7 Mar 86	CA	8	A	1	135	3	139	—
2 May 86								
4 May 86	CA	3	A	—	59	1	60	—
11 Jan 87								
24 Jan 87	CA	27	B	45	387	103	535	—
5 Feb 87								
15 Feb 87	CA	22	B	14	391	92	500	3
23 Feb 88								
9 Apr 88	CA	51	C	1716	120	62	1941	43
28 Nov 88								
14 Dec 88	OR	53	C	667	620	152	1439	—
21 Feb 89								
31 Mar 89	OR	21	C	104	151	34	292	3
All Oregon		83		771	908	186	1875	10
All California		122		1776	1131	326	3279	46***
Oregon + California		205		2547	2039	512	5154	56***

* A = Random selection of both females and males until 25 females were collected.

B = Selection stratified by length (N 5) in <275 mm class, 10 in 275–424 mm class, and 10 in ≥425 mm.

C = Random selection of ≤100 fish (either females or males).

** Level 1 = gross anatomical; Level 2 = histological with anatomical; Level 3 = total fecundity with anatomical and histological.

*** Five females with hydrated oocytes provided by W.W. Wakefield were included in estimate of batch fecundity.

each trawl haul were measured (total length) to the nearest millimeter, sexed, and their gonads classified; some females immediately after capture were also individually weighed to the nearest gram and their ovaries preserved in 10% neutral buffered formalin. Females selected for ovarian preservation were either taken randomly from the trawl catch or selected by length according to a quota for each of three length classes (<275 mm, 275–424 mm, and ≥425 mm) (see Table 1). The preserved ovaries were used to validate our shipboard classification of ovaries, to estimate fecundity, and to provide material for histological descriptions.

Gross anatomical classification of ovaries

Ovaries that were examined onboard the ship were assigned to one of three classes: no yolked oocytes present; yolked oocytes present; and translucent hydrated oocytes present. Ovaries with hydrated oocytes or other yolked oocytes were considered to be in the active state, while those ovaries in which observers saw no yolked oocytes were considered to be in the inactive state. This simple system based on gross anatomical examination of the ovary is more germane for biomass estimation work than are the more complicated systems which involve many more reproductive stages: for example, the seven-stage scale of Hjort (1910), or the five-stage scale of Hagerman

(1952). Eighty percent of the females that we classified using gross anatomical criteria were also classified as active or inactive using histological criteria. The results

were compared to determine the accuracy of identifying active and inactive females by gross anatomical classification.

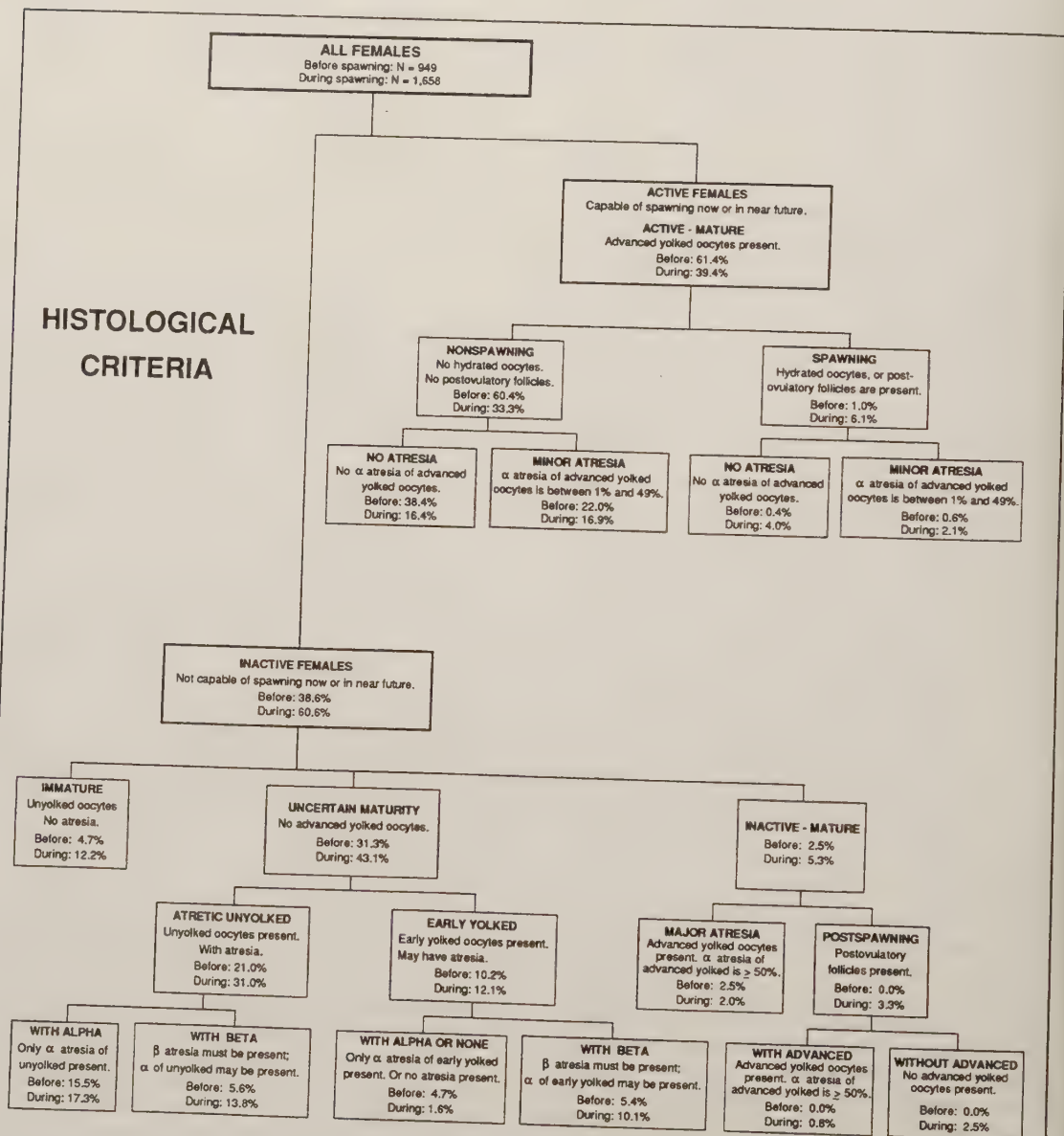


Figure 1

Dendrogram illustrating hierarchical classes of histological criteria of active and inactive ovaries of Dover sole *Microstomus pacificus*. Percentages of females (California and Oregon combined) in each class and subclass taken before (November–December) and during (January–May) the spawning season.

Histological methods

All of the preserved ovaries, regardless of development, had a piece removed for histological analysis. The pieces were dehydrated and then embedded in Paraplast. Subsequently histological sections were cut at 5–6µm and stained with Harris hematoxylin followed by eosin counterstain (H&E). Each ovary was classified histologically in the manner developed for northern anchovy *Engraulis mordax* by Hunter and Goldberg (1980) and Hunter and Macewicz (1980, 1985ab), with a few modifications appropriate for Dover sole ovarian structure. In the ovary we identified the presence or absence of the following: oocytes that have not begun vitellogenesis; oocytes in the first vitellogenic stages (0.15–0.55 mm diameter); advanced yolked oocytes (0.47–1.4 mm diameter) noting any stages of nucleus migration (precursor to hydration); hydrated oocytes; two stages of postovulatory follicles; and the different stages of atresia. The rate at which postovulatory follicles are resorbed in Dover sole is unknown. Hence no ages were assigned to postovulatory follicles.

Histological classification

We used histological analysis of the ovaries to assess the accuracy of our gross anatomical classification into active and inactive states, to define the optimal criteria for distinguishing mature from immature females, and to calculate various indices of spawning activity and postspawning states. The dendrogram (Fig. 1) indicates the histological characteristics used to classify ovaries into active and inactive states. The dendrogram also gives the frequency of the classes in each state for the prespawning period (November–December) and for the spawning season (January–May) using combined data from California and Oregon. The data are also given by cruise and region in Table 2.

Females were classed as active when histological analysis indicated that the ovary contained the sufficient number of advanced yolked oocytes for one spawning. Active females were then separated into spawning and nonspawning classes using additional histological criteria. Spawning females were those which showed histological evidence of past spawning

Table 2

Numbers of female Dover sole *Microstomus pacificus* in various histological subclasses. Listed by location, before or during the spawning season, and mean cruise date (year and month).

Cruise	Inactive									Active						All females	
	Immature			Uncertain maturity						Mature			Mature				
													Nonspawning		Spawning		
	Atretic unyolked			Early yolked			Major atresia	Postspawning		Nonspawning		Spawning					
	Atresia present			No atresia	Atresia present			Advanced yolk		No atresia	Minor atresia	No atresia	Minor atresia				
	α only	β only	α and β	α only	β only	α and β	With	Without									
Oregon																	
Before																	
8512	1	4	0	9	0	0	2	9	5	0	0	20	23	0	0	73	
8812	32	133	2	37	5	37	4	34	15	0	0	316	150	3	4	772	
During																	
8602	0	1	0	9	0	0	2	3	4	0	0	6	12	0	0	37	
8903	23	70	2	16	1	3	7	18	2	1	3	24	14	3	1	188	
8605	1	0	3	4	0	0	5	3	0	4	2	0	0	9	3	34	
Total	57	208	7	75	6	40	20	67	26	5	5	366	199	15	8	1104	
California																	
Before																	
8512	12	10	1	4	0	3	0	3	4	0	0	28	36	1	2	104	
During																	
8701	56	65	11	32	0	7	3	37	11	0	0	115	138	6	9	490	
8702	43	99	8	70	2	11	7	36	10	0	1	91	86	12	10	486	
8603	38	24	8	40	0	1	7	4	3	3	7	1	2	0	0	138	
8803	30	18	4	11	0	4	14	17	3	4	15	31	28	35	11	225	
8605	12	9	3	7	2	1	5	0	0	1	13	4	0	2	1	60	
Total	191	225	35	164	4	27	36	97	31	8	36	270	290	56	33	1503	

(postovulatory follicles present) or imminent spawning (hydrated oocytes or migratory nucleus-stage oocytes present), while the ovaries of nonspawning females showed no evidence of recent or imminent spawning but were capable of spawning in the near future. The fraction of active females classed as spawning was used as a spawning rate index. Spawning performance was also assessed by calculating the mean number of spawning states (postovulatory follicles, hydrated oocytes, migratory nucleus) per female in the spawning class.

Females with ovaries classified as active are considered mature. On the other hand, females with inactive ovaries could be either immature or mature because an ovary may have regressed to an inactive state after the female had attained sexual maturity. We designed our histological classification of inactive ovaries to distinguish as best as possible between mature and immature conditions. Inactive females were grouped into three classes (Fig. 1): immature, uncertain maturity, and inactive-mature. The inactive-mature class included ovaries showing clear histological evidence of past spawning (postspawning subclass) or past maturation of advanced yolked oocytes (major-atresia subclass). Postspawning ovaries contained either postovulatory follicles and no advanced yolked oocytes or postovulatory follicles and mostly atretic advanced yolked oocytes. The fraction of inactive females identified as postspawning was used as an index of the rate at which females passed from the active to the inactive state during the spawning season.

The five major histological classes of active and inactive females were subdivided into atretic subclasses using the first (α) and second (β) stages of resorption as defined by Bretschneider and Duyvene de Wit (1947) and Lambert (1970). One can identify the developmental stage of the oocyte only during the α stage of atresia because the oocyte is completely absorbed by the end of this stage. Subsequent stages (β , γ and δ) involve the resorption of the follicle. Thus, α atresia is of key importance to fecundity studies since the oocyte class can be identified. Subsequent stages may be useful for identifying past spawning activity.

For ovaries containing early yolked or only un yolked oocytes, classification was based solely on presence or absence of the following atresia: β , α of un yolked oocytes, and α of early yolked oocytes (classes immature and uncertain maturity of the inactive females) (Fig. 1).

Ovaries with advanced yolked oocytes were subdivided into two atretic subgroups using the extent of the α atresia of the advanced yolked oocytes: minor atresia, i.e., females with one oocyte to 49% of their advanced yolked oocytes in α ; and major atresia, i.e., 50% or more of the advanced yolked oocytes in α . We showed in anchovy that the probability of spawning

was very low when more than 50% of the advanced oocytes were atretic (Hunter and Macewicz 1985b). Therefore, ovaries with major atresia of advanced yolked oocytes were considered inactive (inactive-mature class) although the ovary contained some advanced yolked oocytes.

Estimation of total fecundity

We used the gravimetric method to estimate total fecundity of Dover sole. Total fecundity (Y_F) was the standing stock of advanced yolked oocytes in the ovary: $Y_F = Z \cdot C$, where Z is the ovary weight in grams, and C is oocyte density (number of advanced yolked oocytes per gram of ovarian tissue). We also measured diameters of 30 of the advanced yolked oocytes in at least one of the 2–5 tissue samples analyzed for each female for which fecundity was estimated. Advanced yolked oocytes were identified, counted, and measured using a digitizer linked by a video camera system to a dissection microscope.

We used the apparent density of yolk in whole oocytes after preservation, when viewed on the television monitor, to discriminate between developmental stages of yolked oocytes. We defined three stages of yolked oocytes: (1) only an initial layer of yolk along the periphery of the oocyte, appearing as a narrow band but not extending over 20% of the distance between the nucleus and the zona pellucida; (2) lightly-packed yolk possibly extending from the periphery to the nucleus with the nuclear area still evident; and (3) yolk dense enough to occlude the nucleus (Fig. 2) which is histologically equivalent to advanced yolked oocytes. Counts of stage-3 oocytes were used to estimate fecundity and measurements to estimate mean diameter of these advanced yolked oocytes.

Alpha atresia of stage-3 yolked oocytes were distinguished from other whole oocytes viewed on the television screen. The yolk within these α -atretic stage-3 oocytes appeared mottled and lighter due to yolk liquefaction and subsequent resorption, whereas in normal yolked oocytes it appeared dense, dark, and in compact globules (Fig. 2). In addition, the zona radiata (chorion, or membrane layers surrounding the oocyte) of the atretic oocytes was indistinct and irregular in appearance. It was not possible to accurately identify atretic oocytes in frozen, thawed, or poorly preserved ovaries. Atretic oocytes were not included in counts of advanced yolked oocytes used to estimate fecundity. To estimate rates of atresia, we recorded the number of α -atretic yolked oocytes in the random sample of 30 stage-3 oocytes measured. The number of α -atretic advanced yolked oocytes divided by 30 was used as an index of the intensity of atresia in all females used for fecundity estimation.

Figure 2

Three stages of preserved whole yolked oocytes of Dover sole *Microstomus pacificus* (stages defined in text). Lower panel also shows migratory nucleus (MN) oocytes, a hydrated (H) oocyte, and an α -atretic advanced yolked oocyte (A). The small air bubble on the hydrated oocyte is an artifact.



Batch fecundity

Batch fecundity was considered to be the number of migratory nucleus-stage oocytes or number of hydrated oocytes in the ovary. We used the gravimetric method to estimate numbers of these oocytes. Migratory nucleus-stage and hydrated oocytes stand out as discrete and easily identified oocyte maturity-classes (Fig. 2). Hydrated ovaries that contained new post-ovulatory follicles were not used to estimate batch fecundity.

We assigned each spawning batch to one of a possible five batch-order designations [1, 2, ($2 < B < U - 1$), ($U - 1$), and U], where B is the batch-order number and U is the total number of spawning batches. The five batch-order designations were defined as follows: first batch (where $B = 1$), nonhydrated, advanced yolked oocytes present and postovulatory follicles absent; second batch (where $B = 2$), one class of postovulatory

follicles and nonhydrated, advanced yolked oocytes present; intermediate batches (where $B > 2$ but less than $U - 1$), two classes of postovulatory follicles and nonhydrated, advanced yolked oocytes present; the penultimate batch ($U - 1$), only two batches were present, one of hydrated and one of migratory nucleus oocytes, with no other advanced yolked oocytes present; and last batch (U), no advanced yolked oocytes present other than a single hydrated batch.

In this classification scheme, we assumed that (1) the presence of a single class of postovulatory follicles indicated one spawning had occurred; (2) the presence of two classes indicated at least two spawnings had occurred; and (3) the absence of postovulatory follicles indicated no spawning had occurred. The assumption of no spawning would not hold if the interval between spawnings was sufficiently long for postovulatory

follicles to be resorbed. We used this batch-order classification system to determine if batch fecundity varied with the order of the spawnings, as it does in some species (Alheit 1986, Hunter et al. 1989).

Estimation of length at 50% mature

We estimated the total length (mm) of female Dover sole when 50% had become mature using histological

criteria. The fraction of females considered to be mature was estimated for 10 mm or for 50 mm length-classes, and the data were fit to a logistic curve (Dixon et al. 1988). We estimated the maturity threshold for females taken off central California and off Oregon, before and during the spawning season. In our analysis, we evaluated the extent to which changes in histological criteria affected the maturity estimate using six sets of histological criteria: (1) advanced yolked

Table 3
Conversion equations for Dover sole *Microstomus pacificus* by state, sex, or season.

Frozen to fresh for length and weight										
Variable		State	Sex	Linear equation $Y = a + bX$					Range of independent variable	
Dependent Y	Independent X			a	b	r^2	F	N		
Fresh length	Frozen length	Cal	All	9.47	1.01	0.99	25,550	251	196-512 mm	
Fresh weight	Frozen weight	Cal	All	0*	1.22	—	10,229	111	54-1551 g	
Fresh weight**	Frozen weight**	Cal	F	0*	1.29	—	19,575	147	76-1263 g	

Length to weight										
Variable		State	Sex	Exponential equation $W = aL^b$					Range of independent variable	
Dependent W	Independent L			a	SE	b	SE	N		
Fresh weight (g)	Fresh length (cm)	Cal	F	0.00198	0.00011	3.45	0.016	1245	11.8-54.7 cm	
		Cal	M	0.00173	0.00018	3.49	0.029	264	18.5-47.8 cm	
		Cal	Unknown					4	12.8-23.5 cm	
		Cal		F, M	0.00198	0.00009	3.45	0.013	1509	11.8-54.7 cm
		Ore	F	0.00141	0.00013	3.53	0.026	991	18.8-57.7 cm	
		Ore	M	0.00156	0.00015	3.51	0.027	457	20.0-52.2 cm	
		Ore	All	0.00159	0.00011	3.50	0.018	1448	18.8-57.7 cm	
Fresh weight** (g)	Fresh length (cm)	Cal	F	0.0038	0.00048	3.27	0.033	1198	11.8-54.7 cm	
		Ore	F	0.0012	0.00026	3.58	0.056	430	26.8-56.4 cm	

Female weight and oocyte volume to ovary weight											
Season	Variable			State	Linear equation $Y = a + bX_1 + cX_2$					Range of independent variable	
	Dependent Y	Independent X_1	Independent X_2		a	b	c	r^2	F		N
Prespawning	Ovary weight (g)	Fish weight** (g)		Ore	9.07	0.013		0.09	38.9	388	122-2017 g
	Ovary weight (g)	Fish weight** (g)	Spher. vol.*** (mm ³)	Cal	-4.67	0.027	37.7	0.54	17.9	30	202-1124 g
				Ore	-34.05	0.036	95.3	0.59	45.85	64	0.33-0.70 mm ³
				Cal+ Ore	-26.06	0.036	76.3	0.59	68.2	94	236-1816 g
Spawning	Ovary weight (g)	Fish weight** (g)		Cal	-7.05	0.032		0.41	826.7	1198	0.33-0.59 mm ³
			Ore	21.79	0.010		0.07	4.2	42	202-1816 g	
			Cal+	-5.88	0.031		0.39	788.0	1240	0.33-0.70 mm ³	
			Ore								14-1736 g

* Intercept not different from 0, line forced through origin.

** Without ovary.

*** Spherical volume = $4/3\pi r^3$; for mean oocyte diameters ≥ 0.86 mm.

oocytes or postovulatory follicles present; (2) early yolked oocytes with β atresia; (3) early yolked oocytes with only α atresia of the early yolked oocytes or no α or β atresia; (4) unyolked oocytes with β ; (5) unyolked oocytes with only α of the unyolked oocytes; and (6) unyolked oocytes with no atresia. The sexual maturity for females identified by criterion 1 is certain, but some females may be excluded if only criterion 1 is used. Criteria 2–5, if added to criterion 1, broaden the maturity definition but increase the risk of misclassification. Criterion 6 is considered by definition to be immature. We evaluated these criteria to determine the optimal histological definition of maturity using a regression analysis of the lengths of females identified by each criterion.

Length, weight, and gonad weight relationships

To enable the reader to convert from one measurement to another, equations are provided to estimate fresh wet weight from frozen wet weight and from length for Dover sole taken in Oregon and central California waters (Table 3). Analysis of covariance indicated that the slope of the regression of the natural logarithms of weight on length did not differ between sexes for either state. The adjusted group mean for males differed from that for females in Oregon (N 1421, $F_{1, 1418}$ 64.87, $P < 0.005$ for length range 225–522 mm) but not in California. The slope of the regression of the natural logarithms of weight on length did not differ between central California and Oregon females but the adjusted group means were different (N 2215, $F_{1, 2212}$ 79.18, $P < 0.005$ for length range 188–547 mm). No difference existed between states in the equations for males. We do not attach too much biological importance to these differences; they could be related to differences in the timing of annual reproductive cycle or our sampling of it. Nonetheless, it seemed preferable to use the relationship for a specific sex or region, so all are listed.

An exponential model was fit to these data sets using a statistical program of weighted nonlinear regression (Dixon et al. 1988) where the weighting factor was the inverse of the variance of fish weight because the variance of fish weight increased with fish length. To compute the variance, fish lengths were divided into several segments, chosen so that within each segment the variance of fish weight was homogeneous. We preferred to obtain the estimates of coefficients directly from the nonlinear fitting so that fish weight could be directly estimated from the exponential model (Table 3).

Freezing of Dover sole caused a 9.47 mm shrinkage in total length, independent of fish length (Table 3). A

sample of 251 Dover sole was measured just after capture and again, after thawing, four months later. The slope of the regression of fresh total length on frozen total length (after thawing) was not statistically different from 1, but the intercept, 9.47 mm, was significant. Freezing of females, with ovary removed, resulted in about a 22% loss in wet weight ($0.22 = 1 - \frac{1}{1.29}$; see Table 3).

We also provided equations to estimate ovary wet weight (g) from female wet weight (g, without ovary). This conversion is important if one wishes to express fecundity as a function of the total weight of the female, because all fecundity relations in this study are expressed as a function of female weight without an ovary. As ovary weight is a function of the developmental state of the ovary as well as the weight of the female, separate equations are provided for the pre-spawning period (November–December) when ovaries are less developed and for the spawning season when they are more fully developed. We also provided multiple regression equations to estimate ovary weight from female weight and the spherical volume of the average advanced yolked oocyte (computed from the mean diameter). These equations are used in the discussion to estimate ovary weight when an ovary contains an entire complement of fully matured advanced yolked oocytes.

Reproductive condition

Accuracy of gross anatomical classification

We rarely misclassified inactive ovaries using gross anatomical criteria. Of the 1272 females classified as inactive, only 14 (1.1%) were identified as active using histological criteria. This error rate is so low that differences could be attributable to clerical errors alone. A more common error in gross anatomical classification was to misclassify females as having active ovaries. One hundred and fifty-nine females (11.9%) were visually classified as having advanced yolked oocytes and were believed to be capable of spawning, while histological analysis indicated that their ovaries were inactive and future spawning was unlikely. The 159 females misclassified as active fell predominantly into two classes: females with ovaries in the early stages of vitellogenesis (40.8%), and females with advanced yolked oocytes with high levels of atresia (30.1%) (Table 4).

Misclassification of the early stages of vitellogenesis as active is expected because the gross anatomical criterion, "yolked oocytes visible," is not exact; observers are bound to differ on whether to include or exclude females that fall near the visible threshold

Table 4

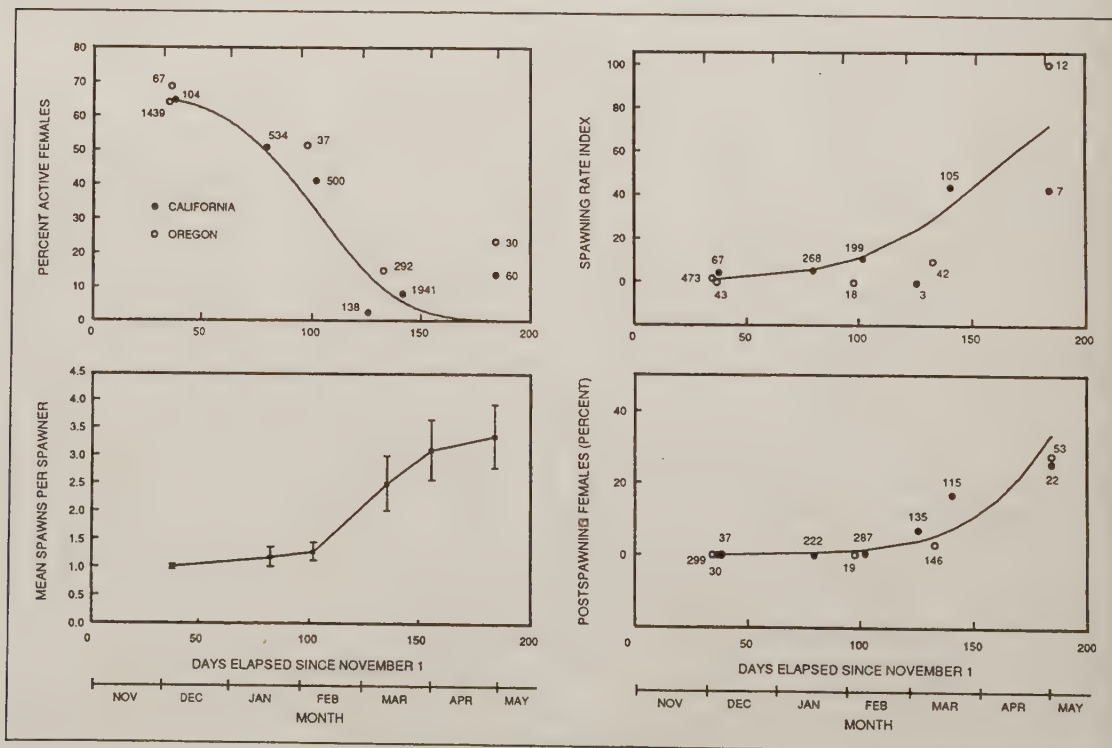
Histological classification of female Dover sole *Microstomus pacificus* with inactive ovaries that were misclassified using gross anatomical criteria as having active ovaries. Data from central California and Oregon are combined.

Collection period	Percentage of females misclassified as active per inactive histological class					Total no. misclassified females
	Immature	Unyolk atretic	Early yolked	Major atresia of adv. yolked	Post-spawning	
Nov-Dec	0.0	2.0	48.9	48.9	0.0	49
Jan-May	4.5	23.6	37.2	21.8	12.7	110
Nov-May	3.1	17.0	40.8	30.1	8.8	159

Figure 3 (below)

Seasonal change in four indices of reproduction in Dover sole *Microstomus pacificus*. Indices are plotted as a function of elapsed time since 1 November; data are combined from different years; California (solid circles) and Oregon (open circles) data were combined to fit trend lines; numbers are the sample size of females. (upper left) Percentage of Dover sole with active ovaries; trend line is a weighted Weibull model (see text Eq. 1). (upper right) Percentage of females with active ovaries which had one or more spawning states; trend line is logistic model

$P = \frac{e^{a+bl}}{1 + e^{a+bl}}$, where $a = -5.678$ and $b = 0.036$. (lower left) Mean number of spawning states in active ovaries; bars are two standard errors of the mean. (lower right) Percentage of females with inactive ovaries identified as postspawning; trend line is logistic model where $a = 8.495$ and $b = 0.042$.



for detection of yolked oocytes in the ovary. An exact criterion, such as oocyte diameter, would be more accurate but would be impractical for production work on the ship. Misclassification of highly atretic ovaries as active is also expected, since α -atretic advanced yolked oocytes are difficult if not impossible to see with the unaided eye. As highly-atretic advanced ovaries were rare in this study, our failure to detect them was a minor systematic error. Under environmental conditions unfavorable to reproduction, however, this could be an error of consequence.

Changes in ovarian condition during the spawning season

The fraction of females anatomically classed with active ovaries

declined over the spawning season as females expended their stock of advanced yolked oocytes. We fitted a weighted Weibull function to the combined California and Oregon data, yielding the equation

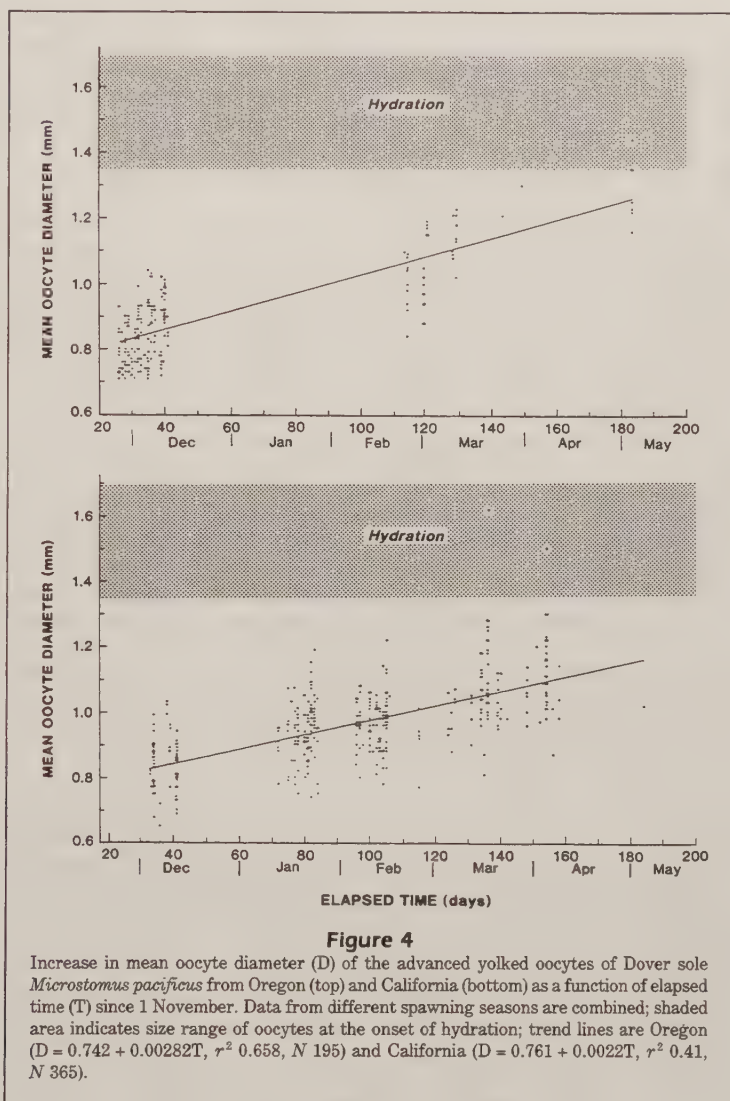
$$P = 0.656 e^{-\left(\frac{t}{111.5}\right)^{3.76}} \quad (\text{Eq. 1})$$

where t is days elapsed since 1 November; P , the fraction active, is weighted by $\frac{N}{P(1-P)}$, and

pseudo r^2 is 0.96. According to the equation, the percentage of females with active ovaries declined from 65% at the onset of the spawning season (about 6 December) to 40% by the end of January; by the end of February only 18% of the females had active ovaries (Fig. 3, upper left).

In California and Oregon, the mean diameter of the stock of advanced yolked oocytes increased steadily from December through April (Fig. 4). Thus reproductively active females continued vitellogenesis throughout most of the spawning season. By March or April the average advanced yolked oocyte is closer to the minimum size at which hydration begins (diameter 1.35 mm). Thus Dover sole may be able to spawn at a higher rate late in the spawning season, because less yolk would have to be added to the advanced oocytes for them to attain the size at hydration.

Only 10 females taken in November–December were classed as spawning on the basis of their ovarian histology (Oregon and California data combined, N 949). They comprised only 1.0% of all females with preserved ovaries taken during this time and only 1.7% of those classed as active. Clearly, spawning is just beginning in November–December in California and Oregon waters. The spawning rate index increased from 1.3% in November–December to 12% by early February; it accelerated at the end of the season with spawning females comprising about 70% of all active females (percent calculated by the trend line in Fig. 3,



upper right). Thus at the end of the season, most of the females with active ovaries had spawned recently. We believe this sharp increase in the index near the end of the season is evidence for a seasonal increase in spawning frequency.

A late seasonal increase also existed in the occurrence of multiple spawning stages within the same ovary. As many as five different past or potential spawning stages could be distinguished histologically in the same ovary: two stages of postovulatory folli-

cles, hydrated oocytes, migratory nucleus oocytes, and other advanced yolked oocytes. These data were expressed as the number of spawning states per spawner (spawns per spawner, Fig. 3, lower left). The average number of spawns per spawner increased from about one in mid-March to about three by early April. These data also indicated that spawning frequency may increase near the end of the spawning season.

The fraction of females with inactive ovaries that were classed as postspawning also increased late in the season (Fig. 3, lower right). This index can be considered a measure of the rate females in the population pass from the active to the inactive state. Although the duration of this stage was unknown, we were certain that it was ephemeral because there were always many fewer females classed as postspawning than the cumulative total of females that had passed from the active to inactive state. This index increased sharply in late-March through April, indicating that the rate females passed into the inactive stage accelerated during the last part of the season.

The sharp increases in the three indices described indicated that the daily production of eggs by the population may be higher in March than February even though fewer fish were spawning. For example, by mid-March (13 March), a half to a third as many females had reproductively active ovaries than in mid-February (10 Feb.). On the other hand, in mid-March as compared

with mid-February, about twice as many females with active ovaries were classed as spawning, and the ovaries of the spawners contained evidence of about twice as many past or potential spawnings. Thus the reproductive output of the reproductively active females in the population in mid-March might be four times that of the active fish in mid-February. If this is true, half the number of active females could produce twice as many eggs per day. This is, of course, sheer speculation because the duration of these spawning stages is unknown. Nevertheless, the data presented in this section collectively suggest that the daily production of eggs by the population may increase near the end of the season even though fewer females are spawning.

Total fecundity

Location of tissue samples

A key assumption underlying the gravimetric method of fecundity estimation is that oocytes are randomly distributed in the ovary. To determine if advanced yolked oocytes are randomly distributed in the ovary, we compared the densities of advanced yolked oocytes in tissue samples taken from five different locations in the ovary of ten females. The location of a tissue sample within the ovary was defined in terms of three

characteristics: longitudinal plane of the ovary (anterior end, middle, and posterior end); cross-sectional plane (interior near the lumen, exterior near the ovarian wall, or interior and exterior combined); and right and left lobes of the ovary. The characteristics of the five ovarian locations along with the mean oocyte density of each location are indicated in Table 5.

Initially we tested the overall effect of location of the tissue sample on oocyte density using two-way ANOVA; the effect of position was insignificant at the 5% level of significance (Table 5, lower). We also tested for possible differences between pairs of location characteristics: posterior end vs. middle; posterior vs. anterior ends of the ovary; right vs. left lobes of the ovary; and interior and exterior sections of the ovary. No significant differences were detectable between any of

Table 5

Effect of location of tissue samples within the ovary of Dover sole *Microstomus pacificus* on oocyte density (number of advanced yolked oocytes per unit sample weight) with mean and standard deviation (SD) and, below, two-way analysis of variance on results.

Position no.	Location in ovary of sample*			N	Oocyte density	
	Lobe	Plane of section			Mean	SD
		Long.	Cross.			
1	Rt	Post	Int & Ext	10	1803.7	468.1
2	Rt	Mid	Ext	10	1801.1	532.0
3	Rt	Mid	Int	10	1754.1	488.6
4	Rt	Ant	Ext	10	1886.1	440.2
5	Lt	Mid	Int	10	1839.3	537.6

Analysis of variance on five locations

Source	DF	SS	MS	F
Fish	9	10,379,034	1,153,226	
Position	4	96,638	24,160	1.373
Error	36	633,493	17,597	
Total	49	11,109,165		

* Long. = longitudinal, Rt = right lobe, Lt = left lobe, Post = posterior end, Mid = middle, Ant = anterior end, Int = internal, and Ext = external.

these four comparisons; F values ranged from 0.01 to 0.14, with the degrees of freedom being 1 and 45 for each comparison. Thus the advanced yolked oocytes in Dover sole are randomly distributed within the ovary, and tissue samples can be taken from any location or lobe without bias.

Optimal number of tissue samples

To develop a procedure for estimating the number of tissue samples needed for estimating total fecundity, we first considered the general fecundity model. The true total fecundity (Y_F) is the condition where all the advanced yolked oocytes in the ovary are counted, and the relation between female weight (W) and fecundity is defined as

$$Y_F = f(W) + A \quad (\text{Eq. 2})$$

where $f(W) = a + bW$, and A is the error term. The variance of A , σ_A^2 , measures the deviation of the data set (Y_F, W) to the model $f(W)$. As it was impractical to count all advanced yolked oocytes in the ovary, Y_F is estimated from counts of oocytes in weighed tissue samples, expressed as oocytes per gram of tissue or oocyte density. The precision of a fecundity estimate can be increased by increasing the number of tissue samples taken per female. On the other hand, if the amount of labor for fecundity work is fixed, then increasing the number of tissue samples per fish would reduce the number of fish that can be sampled. Thus we needed to know the minimum number of tissue samples necessary to guarantee a goodness-of-fit of the model to the data set.

We determined the optimum number of tissue samples by minimizing the variance of sample variance of A ($\sigma^2(s_A^2)$). This procedure led to using the ratio of the variance of oocyte counts between tissue samples within fish (σ_e^2) to the variance around the regression line (σ_A^2), i.e., $\theta = \sigma_e^2/\sigma_A^2$. The smaller the θ , the fewer tissue samples are needed.

Let's denote for the i th fish, $i = 1, \dots, n$,

W_i = fish weight,

Y_{Fi} = total number of advanced yolked oocytes in the ovary,

y_{ij} = advanced yolked oocyte count in the j th tissue sample, $j = 1, \dots, m$,

z_{ij} = weight of the j th tissue sample,

Z_i = formalin wet weight of ovary,

m = number of tissue samples from an ovary,

M_i = maximum number of tissue samples in an ovary,

$\hat{Y}_{Fij}$ = estimate of total number of advanced yolked oocytes in the ovary from the j th tissue sample

$$\left(\frac{y_{ij}}{z_{ij}} \right) Z_i,$$

$\hat{Y}_{Fi}$ = estimated total number of advanced yolked oocytes in the ovary and is used for all analyses in fish fecundity in later sections

$$= \frac{\sum_{j=1}^m \hat{Y}_{Fij}}{m}, \text{ and}$$

$\hat{Y}_{Fi}$ = estimate of total fecundity from the regression model.

We write $\hat{Y}_{Fij}$ as

$$\begin{aligned} \hat{Y}_{Fij} &= Y_{Fi} + (\hat{Y}_{Fij} - Y_{Fi}) \\ &= f(W_i) + A_i + e_{ij} \end{aligned} \quad (\text{Eq. 3})$$

where $e_{ij} = \hat{Y}_{Fij} - Y_{Fi}$. The estimated total number of advanced yolked oocytes in the ovary is

$$\begin{aligned} \hat{Y}_{Fi} &= \frac{\sum_{j=1}^m \hat{Y}_{Fij}}{m} = f(W) + A_i + e_i \\ &= f(W) + \xi \end{aligned} \quad (\text{Eq. 4})$$

and

$$\sigma_\xi^2 = \sigma_A^2 + \left(\frac{M-m}{M} \right) \sigma_e^2. \quad (\text{Eq. 5})$$

Thus the variance around the regression line σ_ξ^2 based upon the data set $(\hat{Y}_{Fi}, W_i)$ is composed of two variance components: one is σ_A^2 and the other is σ_e^2 . The sample counterparts for σ_ξ^2 and σ_e^2 are s_ξ^2 and s_e^2 :

$$s_\xi^2 = \frac{[\hat{Y}_F - f(W)]^2}{n - q} \quad (\text{Eq. 6})$$

is the mean square error from a regression analysis on $(\hat{Y}_{Fi}, W_i)$ where q is the number of regression coefficients and n is the number of fish, and

$$s_e^2 = \frac{\sum_{i=1}^n \sum_{j=1}^m (\hat{Y}_{Fij} - \hat{Y}_{Fi})^2}{n(m-1)} \quad (\text{Eq. 7})$$

is the within-sample variance (Hunter et al. 1985). The estimate (s_A^2) of the variance around $f(W)$ when Y_F is known (σ_A^2) can be estimated by subtraction:

$$s^2_A = s^2_{\xi} - \frac{\left(\frac{M-m}{M}\right) s^2_e}{m} \quad (\text{Eq. 8})$$

According to Hunter et al. (1985), the optimum number of tissue samples can be determined for a given θ ($= s^2_e/s^2_A$), the cost of processing a tissue sample, and the cost of processing a fish. The ratio, $K = s^2_{\xi}/s^2_A$, measured the excess variance which is contributed by taking tissue samples rather than counting every advanced oocyte in the ovary.

We used Dover sole collected during January–February 1987 to determine the optimal number of tissue samples. Two tissue samples were taken from the ovaries of 99 Dover sole. The within-sample variance of oocyte density ($s^2_e = 1053 \times 10^4$) was obtained from an ANOVA, and the linear regression of $\hat{Y}_F$ on W ($\hat{Y}_F = 20,255 + 40.54W$) gave the MSE ($s^2_{\xi} = 18,469 \times 10^4$) (Table 6; Fig. 5, lower middle). Thus θ is 0.058 when calculated from equations (7 and 8) where $m = 2$.

Because M was large (range 200–700), $\frac{M-m}{M}$ was

assumed to equal 1, and s^2_A was computed as $s^2_{\xi} - (s^2_e/2) = 17,942 \times 10^4$. Hence when two tissue samples are used, the variance within tissue samples is only 5.8% of the variance around the fecundity–fish weight regression line. To quantify the excess variance due to subsampling, we computed $K = s^2_{\xi}/s^2_A = 1.03$. This means the variance around the regression line which was based on two tissue samples per fish (Eq. 4) is about 1.03 times that of an equation based on counts of all advanced yolked oocytes in the ovary (Eq. 2). Although the within-ovary variance was small, we recommend counting two tissue samples per female because the cost of processing the second sample was minimal.

Optimal number of females

In addition to the sample allocation based on cost of processing fish and cost of processing tissue samples, the number of females needed for a regression estimate of total fecundity was determined by modifying a procedure suggested by Thigpen (1987) to the 1987 fecundity data for Dover sole. The equation for determin-

ing the sample size (n) for a linear regression was

$$n - 1 = \frac{\left(\frac{1 - r^2}{r^2}\right)}{CV(b)^2} \quad (\text{Eq. 9})$$

Table 6

Within-sample variance ($s^2_e \times 10^{-4}$) from ANOVA and the MSE ($s^2_{\xi} \times 10^{-4}$) from the regression analysis of fecundity ($Y \times 10^{-2}$) and weight of Dover sole *Microstomus pacificus*. California females taken January–February 1987.

Analysis of variance on total fecundity				
Source	DF	SS	MS	
Fish	98	8,559,008	87,337	
Error	99	104,201	1,053	
Total	197	8,663,209		

Analysis of variance on linear regression				
Source	DF	SS	MS	F
Regression	1	2,488,019	2,488,019	134.72
Residual	97	1,791,468	18,469	

Predictor	Coeff.	SD	t
Constant	202.55	32.03	6.32
Fish wt.	40.54	3.49	11.61

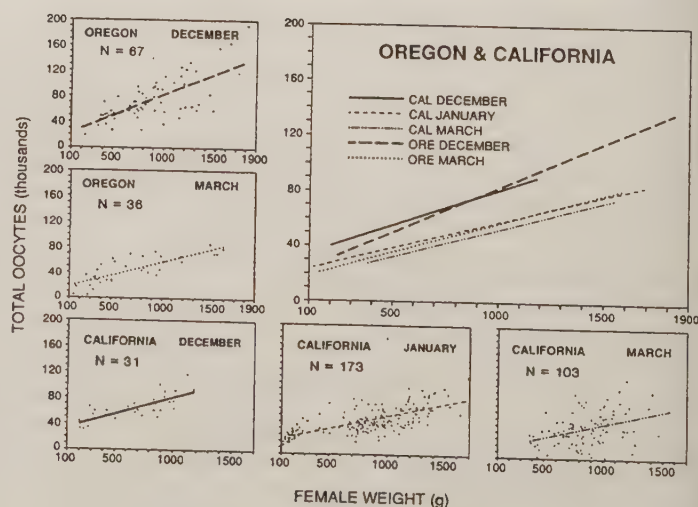


Figure 5

Total fecundity of Dover sole *Microstomus pacificus* as a function of female wet weight in grams (without ovary) for various months taken in central California and Oregon. Each point represents a single female; equations are given in Table 9.

where r^2 is the coefficient of determination, and $CV(b)$ is the coefficient of variation for the regression coefficient (b). The coefficient of determination (r^2) for Dover sole total fecundity and fish weight was 0.58. Thus 73 females are required for a $CV(b) = 0.10$. In conclusion, two tissue samples from each of 70–80 Dover sole females were adequate for expressing the relation between weight and total fecundity, if a $CV(b)$ of about 0.10 is desired.

Relation to ovarian development

The optimum time for estimating potential annual fecundity is early in the spawning season when the probability of spawning is low. Estimates taken in this period may be biased because all oocytes may not have been recruited into the advanced stock of yolked oocytes. In this section, we use Oregon Dover sole taken in November–December to examine the recruitment of oocytes into the advanced stock of yolked oocytes.

If substantial numbers of oocytes are maturing from early-yolked to more advanced stages, one would expect an overlap in the size distributions of oocytes in different development stages. When vitellogenesis of the early yolked oocytes does not continue, one would expect that a gap would develop between the less-advanced and the most-advanced oocytes as the yolked oocytes continued their maturation. In Dover sole, the diameter distributions of stage-1, -2, and -3 oocytes broadly overlap when the mean diameter of the advanced yolked oocytes (stage 3) is less than 0.7 mm (Fig. 6). The extent of overlap declines as the stage-3 oocytes grow from 0.7 mm to 0.8 mm. Separation of the advanced stock (stage 3) from the other vitellogenic stages (1 and 2) becomes complete as the advanced stock grows from 0.8 to 0.9 mm. It appears from this

qualitative analysis that recruitment of stage-2 oocytes into the advanced stock probably ends when the mean diameter of stage 3 is between 0.8 and 0.9 mm.

We conducted a stepwise multiple regression analysis of total fecundity ($\bar{Y}_F$) on mean diameter of the advanced oocytes (D) and female weight (W) for females taken off Oregon in November–December. The coeffi-

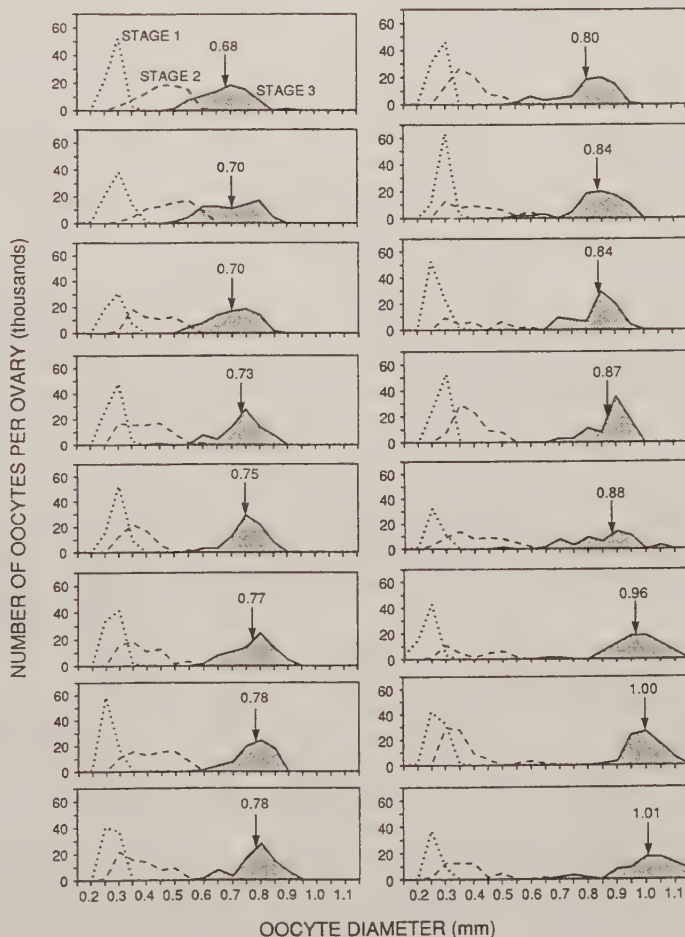


Figure 6

Frequency distribution of oocyte diameter of three vitellogenic oocyte stages in ovaries of Dover sole *Microstomus pacificus*. Each panel represents the ovary from one female. Fish arranged in order of the mean diameter of the advanced yolked oocytes, stage 3 (which is shaded); numbers and arrows indicate mean diameter of stage-3 oocytes. Mean total length was 420 mm and mean ovary-free weight of the females was 868 g. Fish were taken November–December 1988 along the Oregon coastline.

Table 7

Analysis of the relation between total fecundity ($\bar{Y}_F$) of Dover sole *Microstomus pacificus* and gonad-free body weight (W) and the average diameter of the advanced oocytes (D) using stepwise regression with analysis of variance. Specimens from Oregon in November–December 1988.

Stepwise regression				
Step	1	2		
Constant	22,398	-88,768		
Weight (W)	45.4	47.8		
t^*	7.56	8.80		
Diameter (D)		129,893		
t^*		6.01		
S	25,654	23,096		
R^2	27.58	41.69		

Analysis of variance					
Source	DF	SS	MS	F	P
Regression	2	5.68×10^{10}	2.84×10^{10}	53.27	<0.000
Error	149	7.95×10^{10}	5.33×10^{10}		
Total	151	1.36×10^{11}			

Source	DF	Sequential SS
Weight	1	3.76×10^{10}
Egg diameter	1	1.92×10^{10}

* For $P = 0.05$, $1.96 < t < 1.98$, $df \geq 120$.

cient for diameter, as well as the one for weight, was positive and significant (Table 7). Thus the potential annual fecundity was not fully recruited as stage-3 oocytes in some of the Oregon Dover sole taken in November–December, since total fecundity increased with the mean diameter of the oocytes used to estimate total fecundity.

To determine the level of ovarian development (oocyte diameter) at which the full complement of oocytes was recruited into the advanced yolked oocyte class (stage 3), we conducted a series of stepwise multiple regression analyses by successively removing the data by 0.01 mm decrements from the lowermost oocyte diameter class starting at 0.71 mm. This analysis indicated that the threshold for a significant effect of oocyte diameter on total fecundity was between mean diameters of 0.85 and 0.86 mm (Table 8). The multiple regression coefficient for oocyte diameter was significant and positive when females with oocyte diameter

Table 8

Results of stepwise multiple regression of the total fecundity ($\bar{Y}_F$) of Dover sole *Microstomus pacificus* on gonad-free body weight (W) and mean oocyte diameter (D) for a succession of oocyte diameter-classes using the model $\bar{Y}_F = a + b_1W + b_2D$. Specimens taken along Oregon coast November–December 1988. Line separates oocyte diameter-classes where diameter is a significant variable, from those where it is not.

Oocyte diameter class (mm)	Constants		Multiple regression coefficients and their t -ratios for:				
	N	a	Fish weight		Oocyte diameter		r^2
			b_1	t	b_2	t^*	
0.71–1.04	152	-88,768	47.8	8.80	129,893	6.01	0.417
0.72–1.04	148	-90,147	48.3	8.90	130,860	5.87	0.424
0.74–1.04	133	-94,375	49.6	8.34	134,295	5.14	0.415
0.76–1.04	119	-90,710	51.3	7.98	128,688	4.17	0.407
0.78–1.04	105	-83,087	53.4	7.53	118,385	3.16	0.396
0.80–1.04	91	-90,344	55.9	7.29	123,891	2.60	0.400
0.82–1.04	85	-87,274	59.2	7.34	117,459	2.20	0.405
0.83–1.04	81	-111,317	56.9	7.44	145,193	2.77	0.440
0.84–1.04	77	-103,009	58.7	7.55	134,678	2.42	0.460
0.85–1.04	72	-90,464	60.1	7.33	120,166	1.95	0.457
0.86–1.04	67	-38,172	65.3	7.96	60,555	0.94	0.502
0.87–1.04	64	-33,982	63.5	7.30	57,891	0.87	0.482
0.88–1.04	60	-15,721	69.4	7.63	33,456	0.48	0.514
0.90–1.04	46	45,073	82.0	7.92	-40,601	-0.47	0.594
0.92–1.04	34	60,339	84.0	6.92	-58,185	-0.49	0.616

* For $P = 0.05$, t is 1.98 for $df = 120$, 2.00 for $df = 60$, and 2.06 for $df = 25$.

equal to or less than 0.86 mm were included, but was insignificant when only those having a diameter greater than 0.86 mm were considered. We concluded that ovaries in which the advanced stock of yolked oocytes has an average diameter of 0.85 mm or less are not sufficiently developed to be certain that the annual stock is fully recruited. Consequently, to estimate the potential annual fecundity, we used only females in which the average oocyte diameter of the advanced stock exceeded 0.85 mm.

No relationship between oocyte diameter and total fecundity was detected in the females taken off central California during November–December. Oocyte diameter may not have been a significant variable in central California because fewer females were examined and their ovaries were more advanced. In 48% of females from California, advanced yolked oocytes averaged more than 0.85 mm in diameter ($N = 65$), whereas only 34% of the fish taken off Oregon had oocytes that did so ($N = 128$).

Seasonal variation in total fecundity

Total fecundity of Dover sole decreased during the spawning season off both central California and Oregon (Fig. 5). Analysis of covariance indicated that equations expressing the relation between female weight and

fecundity differed within the spawning season (Table 9). The total fecundity for a 1 kg female declined from about 80,000 advanced oocytes in December to about 50–60,000 during the spawning season (Table 9).

To further describe the decline in total fecundity over the season, we also regressed fecundity on female weight and elapsed time since 1 November. In both central California and Oregon the negative coefficients for elapsed time were significant, indicating that total fecundity declined with elapsed time (Table 9). Analysis of covariance indicated that multiple regression equations for California and Oregon were not different (analysis over a similar weight range of 174–1542 g; $F_{1,388} = 1.59$, $P = 0.208$; adjusted mean fecundity for Oregon 57,849, SE 2092; adjusted mean fecundity for California 54,733, SE 1152). When we combined data for the two regions, we found that total fecundity declined on the average about 12% per month. This computation underestimated the actual rate of decline, since it did not take into account females that had spawned all of their advanced yolked oocytes.

Potential annual fecundity

Potential annual fecundity was considered to be equivalent to the standing stock of advanced yolked oocytes in fully developed, prespawning females. We consider

Table 9

Linear regression coefficients, confidence intervals, and estimates for the relationship between female weight (W , ovary-free, in g) and total fecundity ($\hat{Y}_F$) of Dover sole *Microstomus pacificus* from California and Oregon. Analysis of covariance for the effect of season on the relation between total fecundity and weight. Multiple regression coefficients are also given for the effect of elapsed time (T ; days since 1 Nov.) and female weight on total fecundity.

State	Mean date of cruise	Linear regression by month and state								Analysis of covariance for effect of month with weight ranges similar			
		Linear equation $\hat{Y}_F = a + bW$							Regression estimate for 1 kg female	Variables	df	F	P
		a	95% CI	b	95% CI	r^2	F	N					
Oregon	7 Dec 88	17,640	±15,460	65.5	±16.4	0.49	63.9	67	83,140	Weight	1	67.85	<0.005
	3 Mar 89	14,492	±8,530	42.9	±10.6	0.66	67.9	36	57,392	Month	1	20.06	<0.005
										Error	95		
Central California										Total	97		
	8 Dec 85	29,497	±6,121	51.6	±16.1	0.58	42.9	31	81,097	Weight	1	25.20	<0.005
	31 Jan 87	20,154	±6,344	38.9	±6.8	0.42	127.0	173	59,022	Month	2	18.91	<0.005
	23 Mar 88	12,072	±16,924	40.7	±18.6	0.15	18.9	103	52,772	Error	217		
										Total	220		

Multiple regression of total fecundity on weight and days elapsed since 1 November

Multiple regression equation $\hat{Y}_F = a + b_1 W + b_2 T$													
State	a	95% CI	b_1	95% CI	b_2	95% CI	r^2	F	N	W_{min} (g)	W_{max} (g)	T_{min} (d)	T_{max} (d)
Oregon	35,162	±13,378	55.2	±11.2	-237	±104	0.59	74.9	103	147.7	1815.9	33	151
Central California	41,552	±8,142	40.3	±6.4	-224	±63	0.37	92.3	307	120.0	1690.3	34	160

Table 10

Relationship between total fecundity ($\bar{Y}_F$) and gonad-free body weight (g) or total length (mm) for California and Oregon Dover sole *Microstomus pacificus* females meeting specifications for potential annual fecundity estimation (females taken in November–December with average oocyte diameter >0.85 mm and no evidence of past or imminent spawning). Data are compared with Yoklavich and Pikitch (1989) estimates for Oregon.

State	Fecundity and weight							Gonad-free weight (g)	
	Linear equation $\bar{Y}_F = a + bW$							Mean	Range
	a	95% CI	b	95% CI	r^2	F	N		
Oregon	17,640	$\pm 15,453$	65.5	± 16.4	0.488	63.86	67	83,140	870.5 236.0–1815.9
California	29,871	$\pm 12,996$	50.9	± 17.1	0.544	37.06	30	80,771	704.7 202.1–1124.2
Oregon + California	21,124	$\pm 9,248$	62.0	± 10.4	0.504	98.42	97	83,124	819.2 202.1–1815.9

State	Fecundity and length							Total length (mm)	
	Exponential equation $\bar{Y}_F = aL^b$							Mean	Range
	a	95% CI	b	95% CI	Pseudo r^2	F	N		
Oregon	$5.667 \cdot 10^{-6}$	$\pm 1.943 \cdot 10^{-5}$	3.806	± 0.713	0.431	47.03	64	436	298–551
California	$6.101 \cdot 10^{-4}$	$\pm 5.042 \cdot 10^{-3}$	3.020	± 1.380	0.084	2.57	30	423	296–526
Yoklavich & Pikitch**	$1.637 \cdot 10^{-6}$	$\pm 6.928 \cdot 10^{-6}$	4.021	± 0.684	0.818	135.13	32	448	358–550

* Weight is about 1000 g using equation in Table 3.

** Estimated from Yoklavich and Pikitch (1989) original data.

Dover sole to be developed when the average diameter of the advanced oocytes (stage 3) exceeds 0.85 mm; prespawning females are those taken in November–December which show no histological evidence of recent past or of imminent spawning (no postovulatory follicles nor hydrated oocytes present).

Using only specimens that met these specifications, we regressed total fecundity on female weight (without ovary) for females taken in central California and Oregon. The two regression equations were quite similar; when the data are truncated so that the ranges of female weights were equal, no statistical difference existed between California and Oregon. Combining all data, we obtained the general equation

$$\bar{Y}_F = 21,124 + 62.0 W \quad (\text{Eq. 10})$$

where $\bar{Y}_F$ is estimated total fecundity from the regression line, and W is ovary-free female weight in grams. Therefore, the potential annual fecundity for a 1 kg Dover sole is about 83,000 oocytes (Table 10).

Fecundity of Dover sole was estimated recently by Yoklavich

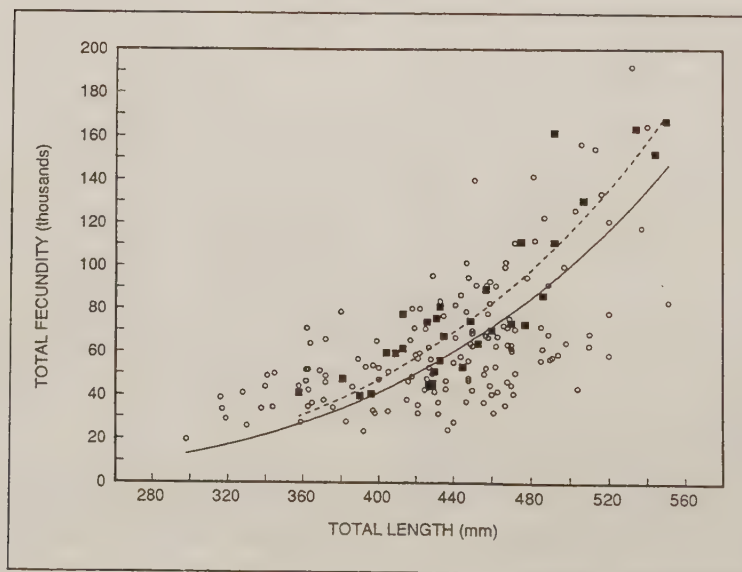


Figure 7

Total fecundity as a function of total length of Dover sole along the Oregon coast for our November–December 1988 data (open circles and solid line) and for data given by Yoklavich and Pikitch (1989) (filled squares and dashed line). Equations are given in Table 10.

Figure 8

Relative frequency distribution of the fraction of the random sample of advanced yolked oocytes measured that were atretic (α stage) from the Dover sole *Microstomus pacificus* females used in estimates of total fecundity shown by state: Oregon females, N 189; California females, N 361.

and Pikitch (1989) for females caught along the Oregon coast. Those authors used an exponential model and expressed annual fecundity as a function of length. The distribution of points in our data broadly overlapped the data of Yoklavich and Pikitch (1989) (Fig. 7). To compare our Oregon data with theirs, we truncated ours so that the length ranges of the two sets coincided and applied an analysis of covariance to log-transformed data. Analysis of covariance indicated that no significant difference existed between the two equations ($F_{1,81}$ 2.03, P 0.158). In Table 10, the exponential equation for fecundity as a function of length is given for our data (not truncated) and for that of Yoklavich and Pikitch (1989). In summary, we found no statistical difference between California and Oregon, nor between our Oregon data and that of Yoklavich and Pikitch (1989).

Atretic losses

In fishes with determinate fecundity, a key question is whether atretic losses during a season constitute an important fraction of the potential annual fecundity. We identified whole atretic oocytes under a microscope while doing our fecundity work. To measure atretic losses, we counted the number of atretic oocytes (α advanced yolked oocytes) occurring in a random sample of 30 advanced yolked oocytes for each of the females used to estimate total fecundity (N 550).

In the fish used to estimate fecundity, the average fraction of advanced yolked oocytes that were atretic was low with the mean 0.015 (SD 0.032, N 361) in California, and even lower in Oregon females (mean 0.0033, SD 0.014, N 189). Atretic oocytes were observed in only 26% of California females and in only 6% of Oregon females (Fig. 8).

The total fecundity of California females was negatively correlated with the fraction of oocytes in the ovary that were atretic. A stepwise multiple regression of female weight, elapsed time, and fraction atretic on total fecundity (Table 11) indicated that the coefficient for the fraction

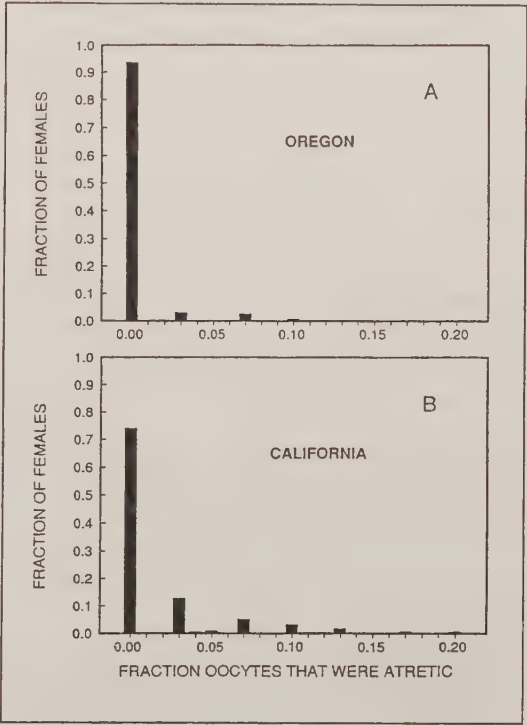


Table 11

Analysis of the relation between total fecundity ($\bar{Y}_F$) of Dover sole *Microstomus pacificus* ovary-free body weight, elapsed days since 1 November, and fraction of atretic oocytes using stepwise regression. Specimens from California.

Stepwise regression			
Step	1	2	3
Constant	23,335	40,296	40,976
Weight	37.7	40.8	41.4
t^*	2.11	14.03	14.23
Elapsed days		-205	-206
t		-7.85	-7.94
Fraction atretic			-63,278
t			-2.17
S	19,317	17,868	17,776
r^2	28.99	39.41	40.20

Analysis of variance					
Source	DF	SS	MS	F	P
Regression	3	7.58×10^{10}	2.53×10^{10}	79.99	<0.001
Error	357	1.13×10^{11}	3.16×10^8		
Total	360	1.89×10^{11}			
Source	DF	Sequential SS			
Weight	1	6.28×10^{10}			
Elapsed days	1	1.15×10^{10}			
Fraction atretic	1	1.49×10^9			

* For $P = 0.05$, t 1.97.

of oocytes that were atretic was significant and negative. According to the equation, when 10% of the advanced oocytes were atretic, total fecundity in a 1 kg female was about 8% lower than when no advanced yolke oocytes were atretic. This analysis indicated that atretic losses of potential annual fecundity occurred, but on a population basis such losses were negligible. No relation between fecundity and atresia existed for Oregon females, probably because atresia was less prevalent in Oregon, with only 6% of females effected compared with 26% in central California.

The ovaries of many more females were examined histologically for atresia ($N = 2607$) than were examined using the anatomical method, because we restricted the anatomical work to the fish used to measure total fecundity. Only 2% of all females examined histologically (Table 2) had ovaries in which 50% or more of the advanced yolke oocytes were in α atresia, but minor atresia was more common. Minor atresia occurred in 52% of the nonspawning California females and in 35% of the nonspawning Oregon females (Table 2).

The histological method was more sensitive than the anatomical one. Alpha atresia of advanced yolke oocytes was detected at least twice as frequently using histological techniques. The histological method was more sensitive because we could detect more subtle changes in oocyte structure and because we scanned about 150 oocytes per ovary, compared with 30 oocytes in the anatomical method. Despite the lack of sensitivity, the anatomical method was valuable because the standing stock of atretic oocytes could be easily estimated and directly related to total fecundity.

The histological evidence indicated that females with α -atretic advanced yolke oocytes were more common in central California waters than off Oregon. However, season and locality were confounded because most females from Oregon were taken prior to the spawning season while most females from California were taken during the season. To determine if either season or locality affected the relative frequency of atretic females, we combined the minor-atresia and major-atresia classes for California and Oregon and fit the

Table 12

Histological determination of number of Dover sole *Microstomus pacificus*, with α atresia of advanced yolke oocytes expressed as a percentage of all females with advanced yolke oocytes taken in central California and in Oregon, beginning (November–December) and during (January–May) the spawning season.

State	Spawning season					
	Beginning		During		Beginning + During	
	%	N	%	N	%	95% CI N
Central California	59.2	71	51.9	617	52.5	47.9–57.2 688
Oregon	36.8	536	49.4	83	38.4	33.8–43.3 619

Table 13

Mean relative batch fecundity for five batch-order numbers (B), from the first batch to the last batch.

Batch-order no. ^a (B)	No. of females	Relative batch fecundity (oocytes/female wt(g))	
		Mean	SD
1	4	2.421	3.810
2	12	11.661	4.410
2 < B < U-1	19	10.489	3.184
U-1	11	12.378	8.035
U	9	7.835	5.723

Analysis of variance on five batch orders

Source	DF	SS	MS	F	P
Batch order	4	371.2	92.8	3.44	0.015
Contrast ^b	1	352.6	352.6	13.08	0.001
Error	50	1347.6	27.0		
Total	54	1718.8			

^aFirst batch spawned, B = 1; last batch spawned, B = U; penultimate batch, B = U-1.

^bComparison of relative fecundity of the first and last batch to the other batches.

stepwise logistic model

$$P = \frac{e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2}}{1 + e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2}} \quad (\text{Eq. 11})$$

to the data (Table 12), where P is the fraction of females with atretic oocytes. The independent variables for location (X_1) are -1 for California and 1 for Oregon, and for season (X_2) are -1 for prespawning and 1 for during spawning. The estimates of coefficients for the equation are $\beta_0 = -0.183$ (SE 0.056) and $\beta_1 = -0.288$ (SE 0.056) (β_2 is not given because effect of season was not significant in an early regression analysis); the estimate of the atresia rate P for California is 0.525 (95% CI 0.479–0.572; Carter et al. 1986) and for Oregon is 0.384 (95% CI 0.338–0.433).

Table 14

Comparison of fecundity between the penultimate batch and the last batch within the same Dover sole *Microstomus pacificus* female.

Female weight (g)	Batch fecundity* (no. of oocytes)	
	Penultimate	Last
270.00	4634	2121
270.00	3716	323
324.50	9374	1025
539.00	11445	2903
703.86	3906	411
713.24	12213	6455
752.11	2843	124
793.54	6134	5856
824.66	7022	3820
1017.70	3621	29
1247.82	11047	250
Mean	677.9	2120
SD	309.8	2355

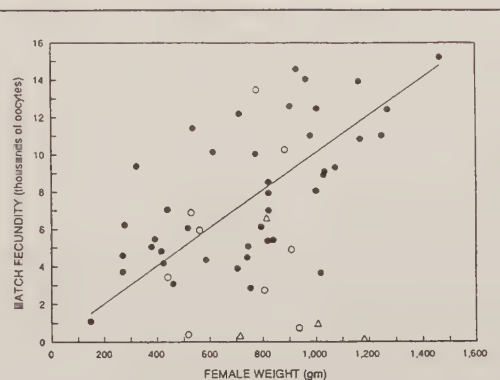
*Paired *t*-test: *t* 4.99, *df* 10, *P* 0.0005.

This computation indicated that the occurrence of females with α atresia of advanced oocytes was significantly affected by locality of the samples but not by season. In short, more California females had one or more α -atretic advanced oocytes in their ovary than did Oregon females.

Batch fecundity

The first step in our analysis of batch fecundity ($\bar{Y}_B$) was to determine if the batch size varied with the order of spawning. Analysis of variance indicated that a significant batch-order effect existed (Table 13). The mean relative fecundity of the first (1) and last spawning batch (U) were significantly lower than the other batches (Table 13).

In eleven females, the only advanced oocytes left in the ovary were two "hydrated" spawning batches (Table 14). Each was in a different stage of development: one was fully hydrated (last batch), and the other was in the migratory nucleus stage (penultimate batch). In all of the eleven females, the last batch was always lower than the penultimate batch. The *t*-test for paired differences confirmed the effect of batch order on fecundity indicated by the ANOVA. The *t*-test also had less potential for bias because we used absolute rather than relative batch fecundity. The *t*-test indicated that the fecundity of the last batch differed from the penultimate batch (*t* 4.99, *df* 10, *P* 0.0005).

**Figure 9**

Batch fecundity of Dover sole *Microstomus pacificus* as a function of female weight (without ovary). Line is $\bar{Y}_B = 10.1W$ for the second through the penultimate spawning batches (filled circles); triangles = first spawning batch; open circles = last spawning batch.

We concluded that the batch size of a female Dover sole did change over the spawning season, with the last and the first batch being lower than the rest.

We determined the relation between batch fecundity and weight using regression analysis. We did not use the first and last batches since they were lower than the rest. The intercept for the regression of batch fecundity on female weight did not differ from zero (*a* 2142; *t* 1.87, *df* 40, *P* 0.07). Therefore we forced the regression line through 0, yielding the relationship $\bar{Y}_B = 10.1W$, where female weight ranged from 148 to 1464 g (Fig. 9). This analysis indicated that the relative batch fecundity of Dover sole is about 10 oocytes per gram ovary-free female weight, except for the first and last batch. The relative fecundity for the first and last batches combined was also about 10 oocytes per gram (1 and U in Table 13). Thus the number of potential spawnings (*S*) per year can be calculated using $S = (\bar{Y}_{FR}/10) + 1$, where $\bar{Y}_{FR}$ is the relative potential annual fecundity ($\bar{Y}_F/W$; $\bar{Y}_F$ from Eq. 10). This means that the average 1 kg female spawns its 83,000 advanced yolked oocytes in about nine batches.

Sexual maturity

To determine the optimal criteria for sexual maturity in female Dover sole, we established six sets of histological criteria for maturity (Table 15). The first set of criteria selects females with either advanced yolked

Table 15

Six sets of histological criteria for female sexual maturity in Dover sole *Microstomus pacificus*, with the mean length of the females in each set. (o) not present; (+) present; (-) not considered.

Criteria set no.	Certainty	Advanced yolked oocytes		Post-ovulatory follicles	Early yolked oocytes		Unyolked oocytes			Mean length (mm)		No. of females Calif. + Oregon (N 2595)	
		with α atresia	no α atresia		with β atresia	only α or none	with β atresia	only α atresia	no atresia	$\bar{x}$	± 2 SE	in class	Cumulative percent
1	Certain maturity	+	+	+	-	-	-	-	-	434	± 3	1343	52
2	Uncertain	o	o	o	+	-	-	-	-	414	± 7	218	60
3	Uncertain	o	o	o	o	+	-	-	-	397	± 11	77	63
4	Uncertain	o	o	o	o	o	+	-	-	379	± 6	279	74
5	Uncertain	o	o	o	o	o	o	+	-	350	± 5	432	90
6	Certain immaturity*	o	o	o	o	o	o	o	+	297	± 10	246	100

* Defined as certain immaturity because no histological evidence exists for maturity.

oocytes or postovulatory follicles. The sexual maturity of these females is certain, but some mature females may be excluded if only the first set of criteria are used. Criteria sets 2 to 5, if added to the first set, broaden the maturity definition to include females having ovaries in the earliest stages of vitellogenesis and those showing possible signs of past reproductive activity (β - or α -stage atresia). Each additional criteria set that one might add to the first set increases the risk that immature fish will be classed as mature. Females in set 6 are considered to be immature because they have none of the characteristics mentioned in the other five sets.

Use of β atresia as a possible sign of past reproductive activity seems justified. Females with early yolked oocytes and β atresia (set 2) were larger on the average than those with no β atresia (set 3; t 2.45, P 0.015, df 293); and females with unyolked oocytes and β atresia (set 4) were larger than those with only α atresia of the unyolked (set 5; t 7.69, P < 0.001, df 709). In addition, the ranking of criteria sets based on our intuitive appraisal of the risk of classification error is largely borne out by the length distributions of the females identified by the criteria set, since mean length decreased with criteria set number (Fig. 10).

To estimate the length at which 50% of the Dover sole are mature (ML_{50}) using all six histological criteria sets, we first used a maturity algorithm to estimate the fraction of fish that were mature in a given length-class. This algorithm is a regression method similar to those used to construct age-length keys (Bartoo and Parker 1983, Kimura and Chikuni 1987).

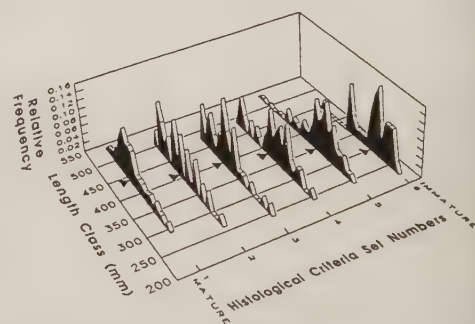


Figure 10

Length distribution of female Dover sole *Microstomus pacificus* identified by six sets of histological maturity criteria, ranging from criteria set 1 where maturity is certain, to set 6 where all females are considered to be immature (see Table 15). Females captured in November–December in California and Oregon; filled triangles indicate mean length of females.

This analysis was based on two equations. The first equation was

$$q_{ji} = q_{m|i} q_{j|m} + (1 - q_{m|i}) q_{j|im} \quad (\text{Eq. 12})$$

where q_{ji} is the fraction of fish of length-class j in the i th criteria set; $q_{j|m} = q_{j|1}$ and $q_{j|im} = q_{j|6}$ because the criteria set 1 consists of all mature (m) fish and the criteria set 6 consists of all immature (im) fish; and $q_{m|i}$ the overall fraction of mature fish in the i th cri-

teria set. The second equation assumed that $q_{m|i}$ changed linearly with criteria set number i :

$$\hat{q}_{m|i} = b_1 + b_2i. \tag{Eq. 13}$$

Combining equations (12) and (13) results in the final equation

$$y_{ij} = b_1x_{1j} + b_2x_{2j} \tag{Eq. 14}$$

where $y_{ij} = q_{j|i} - q_{j|im}$,
 $x_{1j} = q_{j|m} - q_{j|im}$, and
 $x_{2j} = i(q_{j|m} - q_{j|im})$.

For each criteria set i , we obtained the estimate of the fraction of mature fish ($q_{m|j|i}$) in each length-class j as

$$\hat{q}_{m|j|i} = \hat{q}_{m,j|i} / \hat{q}_{j|i} = [\hat{q}_{m|i}q_{j|m}] / \hat{q}_{j|i}.$$

We then obtained the estimated number of mature fish of length-class j in the criteria set i ($\hat{N}_{m|j|i}$) as the product of the total number of fish at length-class j ($N_{j|i}$) and the estimated fraction of mature fish at length-class j ($\hat{q}_{m|j|i}$):

$$\hat{N}_{m|j|i} = N_{j|i} \hat{q}_{m|j|i}.$$

The summation of $\hat{N}_{m|j|i}$ over all criteria (i) is the total number of mature fish at length-class j ($\hat{N}_{m|j} = \sum_i \hat{N}_{m|j|i}$). The total number of fish in length-class j ($N_j = \sum_i N_{j|i}$) and the number of mature fish ($\hat{N}_{m|j}$) were used to estimate ML_{50} for all females taken before the onset of spawning (California and Oregon data combined) using BMDPLR (Dixon et al. 1988).

We compared the above estimate with the ML_{50} for each of the five maturity definitions created by including progressively more criteria sets (Table 16). When the definition of sexual maturity is expanded by progressively adding criteria sets 2 to 5 to the definition, the ML_{50} decreased for each additional set of criteria added. Our estimate of ML_{50} from the model was 332 mm and is most similar to maturity definition IV in Table 16. Thus, definition IV is the preferred histological definition of maturity because it is probably the least biased.

Inspection of Table 16 also indicated that the ML_{50} is always greater when measurements are made during the reproductive season than before it begins, regardless of the number of criteria sets used to define sexual maturity. This implied that during the spawning season the ovaries of some postspawning females are reabsorbed to the extent that they become indistinguishable from females defined as immature. Thus maturity should be estimated prior to the onset of spawning, and the definition of maturity should be broader than definition I.

We believe the preferable estimate of ML_{50} is one based on the maturity algorithm because it uses all the histological data, while those based on definitions use only a portion of it. The maturity algorithm should be applied only to data taken before the spawning season, since data collected later in the season will be biased. This method demands detailed histological classification which may be too costly for many purposes. Definition III could be used if tissue were examined microscopically or with a powerful hand lens, and it gives an ML_{50} value close to that provided by the model.

Table 16

Estimated length at which 50% of Dover sole females are sexually mature, using six histological definitions of ovarian maturity and a maturity algorithm that uses all data. California and Oregon data are combined; length at 50% mature estimated using logistic model (Dixon et al. 1988).

Definition no.	Histological criteria sets incl. in maturity definition ^a	Before spawning (N 854 females)			During spawning (N 1321 females)		
		Length at 50% mature (mm)	No. of mature females		Length at 50% mature (mm)	No. of mature females	
			N	% of females		N	% of females
I	1	373	541	63	419	568	43
II	1, 2	361	582	68	396	692	52
III	1, 2, 3	348	626	73	391	720	54
IV	1, 2, 3, 4	332	669	78	348	917	69
V	1, 2, 3, 4, 5	258	810	95	255	1184	90
Maturity algorithm	1, 2, 3, 4, 5, 6	332	691 ^b	81 ^b	389	742 ^b	56 ^b

^aFrom Table 15.
^bEstimated from maturity algorithm.

Table 17

Final maturity thresholds and logistic model parameters* for female Dover sole *Microstomus pacificus*, taken before the spawning season in California, Oregon, and the two states combined.

Region	Maturity definition	50% mature	95% CI	a	SE	b	SE	N
California	IV	298	215-391	-14.412	4.374	0.0483	0.0149	104
Oregon	IV	336	322-351	-9.268	0.806	0.0276	0.0022	750
California + Oregon	Maturity algorithm	332	305-367	-14.960	1.239	0.0450	0.0036	854

$$* P = \frac{e^{a+bL}}{1 + e^{a+bL}}$$

We combined data from Oregon and California in this analysis because sample sizes (before spawning) were inadequate for application of the model separately. However, in Table 17 we provide estimates and fitting parameters based on definition IV for each region as well as those based on the model using the combined data. The ML_{50} estimated for definition IV was lower in California than in Oregon. However, analysis of covariance of the log transformation of fraction mature,

$\ln\left(\frac{q_m}{1-q_m} + 1\right)$, on length and locality indicated that

the difference between states was not significant (P 0.625, F 0.26). Thus our ML_{50} estimate for Dover sole along the California and Oregon coasts is 332 mm with 95% CI of 315-349 mm (Carter et al. 1986; Fig. 11). The ML_{50} we estimated from data in Hagerman (1952) for Dover sole from the Eureka California fishery is high (363 mm) compared with our final estimate for Oregon and California coasts (Fig. 11). However, Hagerman collected his specimens during the spawning season, and his estimate is similar to the ML_{50} for females taken during the spawning season (Definition IV, Table 16).

Discussion

Validation of fecundity assumptions

In the Introduction, we specified four assumptions required for an unbiased estimate of annual fecundity in Dover sole. These assumptions were that (1) fecundity was determinate; (2) potential annual fecundity was equivalent to actual fecundity; (3) females used to estimate annual fecundity had not spawned; and (4) recruitment of oocytes into the advanced stock of yolked oocytes had ceased for the season. The following is a review of the evidence for the four assumptions.

Five lines of evidence support the assumption of determinate fecundity for Dover sole: (1) in mature

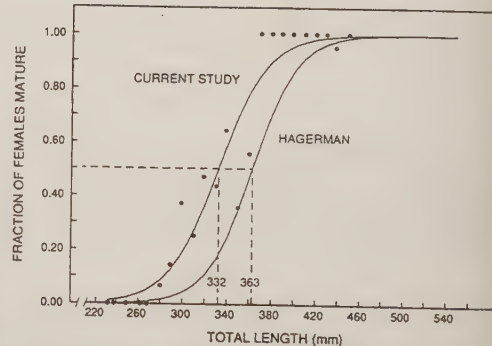


Figure 11

Fraction of female Dover sole *Microstomus pacificus* that were sexually mature as a function of total length. Points are for 10 mm length-class intervals; the fraction mature per length-class was assigned using maturity algorithm; data were from California and Oregon in November-December; logistic parameters are in Table 17. Present study is compared with Hagerman (1952), line only (logistic curve parameters, a -17.854, b 0.0450).

ovaries (mean diameter of advanced oocytes >0.85 mm), a hiatus existed between the advanced stock of mature oocytes and smaller, less mature oocytes; (2) total fecundity declined over the spawning season; (3) total fecundity was lower in females having postovulatory follicles; (4) the mean diameter of the advanced oocytes increased over the spawning season; and (5) our analysis of the order of spawning batches was consistent with the determinate fecundity assumption.

The second assumption, lack of significant atresia, also was supported by our analysis. Overall, atretic losses of advanced oocytes were negligible during the years of our study. Multiple regression analysis indicated that atresia had a small but significant effect on total fecundity of the California females that had

atretic oocytes. A few females suffered substantial losses in total fecundity, but such fish were rare and they had little effect on population means. Histological and anatomical evidence indicated that females with α -atretic advanced yolked oocytes were more common in central California than in Oregon waters. Atresia might be more common in central California Dover sole because bottom sediments are contaminated. Alternatively, females with atretic ovaries may be more common in central California waters because they are living near the southern end of their range where food supply and other habitat conditions may be less than optimal. Both explanations seem equally plausible at present.

The third assumption, that females used to estimate potential annual fecundity have not spawned in the current reproductive year, would be rejected for females taken in January through May. The assumption probably held for the females used to estimate annual fecundity in November–December because only 2.9% of the females from California and only 1% of the females in Oregon showed any histological signs of past or imminent spawning. The few females that showed histological signs of spawning were not used, of course, to estimate annual fecundity. Spawning may have gone undetected in some of the females used to estimate fecundity since postovulatory follicles are eventually resorbed. This does not seem likely for the November–December case because the spawning season had just begun and resorption is probably slow at the low temperatures of Dover sole spawning habitat.

Our fourth assumption, that all the oocytes that constitute the potential annual fecundity were included in our oocyte counts, is supported by two lines of evidence. The first is that no positive correlation existed between the mean diameter of the advanced oocytes and total fecundity. Such positive correlations were eliminated by excluding all ovaries in which the mean diameter of the advanced oocytes was less than 0.86 mm. A positive correlation between diameter and fecundity existed when all ovaries were considered (range in mean diameter of the advanced oocytes, 0.71–1.04 mm). This is evidence that recruitment of oocytes into the advanced class continued until the advanced stock was well separated from early vitellogenic oocytes (stages 1 and 2, Fig. 6). The second source of evidence is the form of the oocyte size-frequency distribution. A prominent gap between stage-2 and stage-3 oocytes existed when the mean diameter of stage-3 oocytes was between 0.84 and 0.96 mm (Fig. 6). The absence of significant numbers of oocytes in the intervening diameter classes (0.55–0.65 mm) indicates maturation of oocytes across this range either had ceased or was proceeding at a very slow pace. We conclude that recruitment of significant numbers of oocytes into the advanced stock probably ceases in

Dover sole when the mean diameter of the advanced stock is between 0.86 and 0.96 mm.

Some authors working with other species (Hislop and Hall 1974 on *Melanogaster merlangus* (L.), Horwood and Greer Walker 1990 on *Solea solea*) consider all yolking oocytes to comprise the potential annual fecundity. In Dover sole this would mean that in addition to stage 3, the most advanced yolked oocytes, stages 1 and 2 would also be used to estimate annual fecundity. Such broad criteria are acceptable if all oocytes that began vitellogenesis ultimately become a part of the mature stock of oocytes that are spawned. This was not the case in Dover sole because oocytes in the early stages of vitellogenesis (stages 1 and 2) occurred in nearly all mature ovaries, including those in which some of the batches had already been spawned. The fate and dynamics of these small partially-yolked oocytes in advanced ovaries is uncertain; their numbers might either decrease due to resorption, increase and become part of next year's production, or remain in stable numbers until later in the year. It would seem impractical to adjust estimates of potential annual fecundity based on all vitellogenic oocytes for the fraction of those oocytes which do not continue vitellogenesis. Therefore, we believe use of the more mature yolked oocytes for estimating the potential annual fecundity is preferable.

An important implication of our discussions of the third and fourth assumptions is that timing the sampling of females is a critical element in estimating potential annual fecundity: Sample too early in the reproductive cycle and the ovaries are not sufficiently mature; sample too late and spawning is prevalent. The optimal time to sample Dover sole ovaries is when the average diameter of the advanced stock is between 0.86 and 1.1 mm (Fig. 12). When the diameter is less than 0.86 mm, the numbers of advanced oocytes are still increasing (indicated by the t value for the diameter coefficient in the fecundity equation, Fig. 12). When the diameter exceeds 1.1 mm, 20% or more of the females show histological signs of past or imminent spawning, and the assumption of no spawning cannot be safely made.

Spawning rates and reproductive energetics

The spawning season of Dover sole was protracted with postovulatory follicles occurring as early as December and hydrated oocytes as late as May, indicating a season of six months. This is a long season for a fish of determinate fecundity, since typically they are high-latitude species with short, 1–2 month spawning seasons. Batch fecundity was low, averaging about 10 oocytes per gram female weight, except for the first and last batch which average about 5 oocytes per gram. Dover sole spawn about nine times during their

protracted spawning season. Vitellogenesis does not cease when spawning begins, but rather it continues throughout most of the season as the advanced stocks of yolked oocytes are matured and spawned. Spawning frequency appears to increase near the end of the season. This may cause a higher daily production of eggs by the population in late-March or April than in February, even though fewer females have active ovaries in April.

To estimate reproductive effort of Dover sole, we calculated the hypothetical weight of the ovary when the entire advanced stock of oocytes had completed vitellogenesis and hydration had begun. The weight is hypothetical because a Dover sole ovary never contains a full complement of completely yolked oocytes, since vitellogenesis of the smaller advanced yolked oocytes continues after a female begins spawning. To compute the hypothetical weight, we assumed that all oocytes completed vitellogenesis when their average diameter was 1.5 mm. Hydration begins when the advanced yolked oocytes have a mean diameter of 1.3–1.7 mm. We estimated the gonad weight of a 1000 g female with oocytes having a mean diameter of 1.5 mm, using an equation in which gonad weight was expressed as a function of fish weight and volume of the average advanced oocyte (1.5 mm diameter has a volume of 1.77 mm^3 ; California plus Oregon data; Table 3). The ovary was estimated to weigh 144 g, or about 14% of the body weight. In other words, the annual reproductive effort of Dover sole was about 14% per year, and this effort was distributed over about nine spawnings averaging about 1.6% of their body weight per spawning. Gonad weight was considered to be a measure of reproductive effort by Gunderson and Dygert (1988); but they did not adjust the gonad weight for the full complement of yolk, and consequently their estimates are not comparable to these.

Assessment of sexual maturity

Our estimates of length at 50% mature (ML_{50}) were higher when females were taken during the spawning season than when they were sampled before spawning began, regardless of the histological criteria used. Thus, during the spawning season ovaries of some post-spawning females had regressed far enough that they were histologically indistinguishable from immature

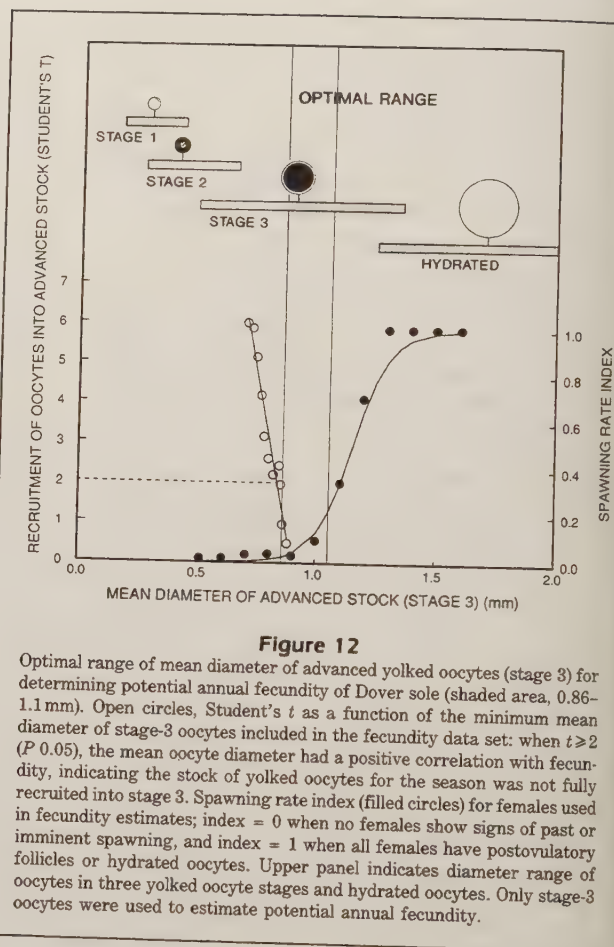


Figure 12

Optimal range of mean diameter of advanced yolked oocytes (stage 3) for determining potential annual fecundity of Dover sole (shaded area, 0.86–1.1 mm). Open circles, Student's t as a function of the minimum mean diameter of stage-3 oocytes included in the fecundity data set: when $t \geq 2$ ($P \leq 0.05$), the mean oocyte diameter had a positive correlation with fecundity, indicating the stock of yolked oocytes for the season was not fully recruited into stage 3. Spawning rate index (filled circles) for females used in fecundity estimates; index = 0 when no females show signs of past or imminent spawning, and index = 1 when all females have postovulatory follicles or hydrated oocytes. Upper panel indicates diameter range of oocytes in three yolked oocyte stages and hydrated oocytes. Only stage-3 oocytes were used to estimate potential annual fecundity.

females. This finding has two important implications: First, it indicates that even the broadest histological criteria, based on analysis of H&E sections, will not identify all postspawning females; second, it means that estimates of length or age at first maturity should always be conducted prior to the onset of spawning, when postspawning females with highly regressed ovaries are rare.

Another limit to our ability to assess sexual maturity is that we do not know how many of the females that begin vitellogenesis actually complete it during the current reproductive season. Dover sole ovaries with oocytes in the early vitellogenic stage occurred throughout the spawning season as well as before it began, indicating some females that begin vitellogenesis may not reach sexual maturity in the current

season. At this time, it is an arbitrary choice to consider as mature all females with vitellogenic ovaries or only those with advanced yolked oocytes. Our analysis showed that this arbitrary decision had a pronounced effect on ML_{50} estimates. Thus the criteria for maturity estimates should be precisely specified. It is particularly important to specify the minimum level of oocyte development necessary for a female to be considered as mature. Our preferred definition of maturity included females in the early stages of vitellogenesis with yolked oocytes as small as 0.18 mm diameter, and also included some females without vitellogenic oocytes (maturity IV, Table 16). Those females without vitellogenic oocytes had β atresia in the ovary. We believe that the presence of some β atresia is an inevitable consequence of the resorption of an active ovary or ovulation.

No discussion of sexual maturity would be complete without mentioning the gross anatomical systems used to classify ovaries, because they are the chief method used by fishery biologists to measure sexual maturity in marine fishes. Using gross anatomical criteria, we accurately separated active ovaries (advanced yolked oocytes present) from inactive ovaries (no advanced oocytes) with classification errors of 1–12%. Determining sexual maturity is a far more difficult task, however. Identification of mature females using gross anatomical methods has the same problems with post-spawning and early vitellogenesis criteria as histological methods, but the potential for bias is greater. Anatomical criteria are less accurate and may be detectable for shorter periods than histological ones. For these reasons, differences between maturity studies should be interpreted with caution, especially when done by different observers, or with different methods, or when sampling at different times of the year. Many investigators have not been particularly careful to restrict sampling to early in the spawning season. The tendency will be to overestimate the ML_{50} using anatomical methods, especially when samples are taken midseason.

In an earlier paper on Dover sole, Hunter et al. (1990) concluded that size at 50% mature in Dover sole from central California in the 1980s differed from that of Dover sole in northern California in the late 1940s as determined by Hagerman (1952). Although a statistical difference existed between these two data sets, we are inclined to dismiss this difference, since it could be due to differences in criteria and sampling times. Similarly, Yoklavitch and Pikitch (1989) speculated that size at 50% maturity of Oregon Dover sole has changed because their estimate of maturity differed from Harry (1959). We believe that this difference also could easily be due to differences in criteria and timing of sampling. Our analysis of histological criteria for maturity clearly

shows that differences in criteria or timing of sampling can produce differences in the ML_{50} as large as any of those seen in the Dover sole literature.

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Citations

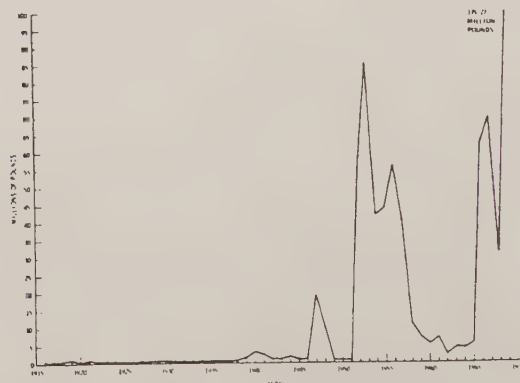
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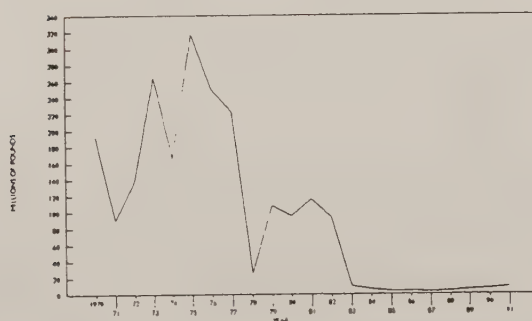
Anchovy harvested by the live bait fishery are not landed but kept alive for sale to anglers as bait. Transactions between buyers and sellers of live bait take place either at sea or at bait wells tied up at docks. Live-bait dealers generally supply bait to partyboats on a contract basis and receive a percentage of the fees paid by passengers. Bait is also sold by the "scoop" to anglers in private vessels.

Anchovy landed by the non-reduction (other than live bait) fishery are used as dead frozen bait, fresh fish for human consumption, canned fish for human consumption, animal food, and anchovy paste.

Reliable records of California landings of northern anchovy date from 1916. Landings were small until scarcity of Pacific sardine caused processors to begin canning anchovies in quantity during 1947, when landings increased to 9,464 tons. In order to lower the quantity of anchovies being reduced to fish meal, the California Fish and Game Commission required each processor to can a large proportion of the harvest (40–60 percent depending on can size). Anchovy landings declined with the temporary resurgence of sardine landings through 1951. Following the collapse of the sardine fishery in 1952, anchovy landings increased to 42,889 tons in 1953, but subsequently declined, largely due to low consumer demand for canned anchovy and increased sardine landings. Landings remained low through 1964. During the early years of the anchovy fisheries (1916–1964), anchovy were harvested almost exclusively by California fishermen. Mexico did not begin harvesting anchovy until 1962.



California commercial landings of northern anchovy, 1916–1969.



California commercial landings of northern anchovy, 1970–1991.

PELAGIC WETFISH

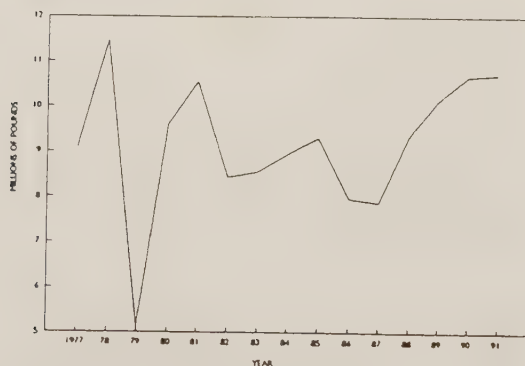
NORTHERN ANCHOVY

History of the Fishery

Northern anchovy (*Engraulis mordax*) are exploited by three separate fisheries in both California and Mexico. Anchovy landed by the reduction fishery are converted to meal, oil and soluble protein products that are sold mainly as protein supplements for poultry food but also as feed for farmed fish and other animals. Meal obtained from anchovy is about 65 percent protein compared to about 50–55 percent for meal from other fishes.

Beginning in 1965, the California Fish and Game Commission managed anchovy on the basis of a reduction quota. This quota has been taken by a fleet of approximately forty small purse seine vessels known collectively as the "wetfish" fleet, which fishes for other species in addition to anchovy. Anchovy landed for reduction in California increased from 171 tons in 1965 to 27,330 tons in 1966, and ranged from 13,786 to 92,893 tons per year during 1966-1972, and from 80,855 to 155,966 tons per year during 1973-1977. In response to a decrease in the price of fish meal, landings declined to an annual average of 51,223 tons during 1979-1982. Reduction landings have been extremely low since 1983, largely as a result of low prices offered to fisherman.

The non-reduction fleet in recent years has consisted of about eighteen boats that are distributed along the California coast to serve the principal sport fishing markets, mostly in southern California.



California landings of northern anchovy for live bait, 1977-1991.

The live bait boats fish for a variety of species, but anchovies comprise approximately 85 percent of the catch. Historically, the anchovy live bait catch ranged from 4,000 to 8,000 tons per year and averaged 5,748 tons annually in recent years. Non-reduction (other than for live bait) landings averaged about 2,189 tons per year from 1965 to 1989 and, since 1985, have exceeded reduction landings in California because of a major decline in the reduction fishery.

Anchovy landed in Mexico are used primarily for reduction, although a small amount is used as bait. Mexico's harvesting and processing capacity increased significantly in the late 1970's when several large seiners were added to the fishing fleet and a large reduction plant was constructed in Ensenada. Mexican landings reached a high of 284,975 tons in 1981, fell to 196,078 tons in 1982, and have ranged from 87,024 to 136,594 tons per year since 1983. The fishery ceased operation in 1991.

The U.S. northern anchovy fisheries have been managed by the Pacific Fishery Management Council since 1978. Current regulations impose no numeric limit on live bait catch and provide a 7,711 ton quota for other non-reduction uses. The regulations also specify an optimum yield for the reduction fishery ranging from zero to 220,000 tons depending on the size of the spawning population.

Although the northern anchovy is harvested by fisheries in Mexican as well as U.S. waters, there is no bilateral management agreement with Mexico. In the absence of such an agreement, fishery managers in the U.S. assume that U.S. fisherman are entitled to 70 percent of the total optimum yield and quotas are set on this basis. The assumption is based on an estimate that 70 percent of the shared northern anchovy resource is, on average, found in U.S. waters. The Mexican fishery is managed independently and is not restricted by a quota.

Economics explain a great deal about the current dynamics of anchovy fisheries in California, because the fisheries are more limited by prices and markets than by biological constraints. The price paid to fisherman for anchovy landed as live bait has been about \$618 per ton. On this basis, revenues in the live bait fishery during 1989 were about \$3.1 million. Although prices and revenues for live bait tend to be surprisingly high, annual catches have been modest because of market limitations.

During 1980 to 1988, the price paid for anchovy landed for non-reduction purposes other than live bait averaged about \$261 per ton. As with live bait, market limitations have resulted in modest annual catches despite relatively high prices paid to fishermen.

The average price for anchovy landed by the U.S. reduction fishery during 1974 to 1988 was about \$55 per ton, but the price paid during 1988 was only \$29 per ton. Low prices, as well as market problems, have prevented a significant U.S. reduction fishery in recent years.



Northern anchovy, *Engraulis mordax*.

Status of Biological Knowledge

Northern anchovy are distributed from the Queen Charlotte Islands, British Columbia to Magdalena Bay, Baja California. The population is divided into northern, central, and southern subpopulations or stocks. The central subpopulation ranges from approximately San Francisco, California to Punta Baja, Baja California, with the bulk being located in the Southern California Bight.

Northern anchovies are small, short-lived fish typically found in schools near the surface. They rarely exceed four years of age and seven inches total length, although individuals as old as seven years and nine inches have been recorded. There is a great deal of regional variation in age composition (number of fish in each age group) and size at age with older fish and larger fish found at relatively offshore and northerly locations. In warm years relatively old and large fish are found farther north than during cool years. These patterns are probably due to northern and offshore migration of large fish, regional differences in growth rate, and water temperatures. Northern anchovies in the central subpopulation are typically found in waters that range from 54° to 71° F.

Information about changes in anchovy abundance during 1780 to 1970 is available from scales counted in sediment cores from the Santa Barbara basin. These data indicate significant anchovy populations existed throughout the time period and that biomass levels during the late 1960's were modest relative to those during most of the 19th and early 20th centuries.

The age at which northern anchovy become vulnerable to California fisheries depends on the location of the fishery and type of fishery. Fish become vulnerable to the inshore live bait fishery at an earlier age than they become vulnerable to the reduction fishery. However substantial numbers of zero and one year old fish are taken by both fisheries in most years.

Anchovy are all sexually mature at age two. The fraction of one-year-olds that is sexually mature in a given year depends on water temperature and has been observed to range from 47 to 100 percent. They spawn during every month of the year but spawning increases during late winter and early spring and peaks during February to April. Spawning has been observed over a temperature range of 54° to 71°F. Individual females spawn batches of eggs throughout the spawning season at intervals as short as seven to ten days. The eggs are found near the surface, and require two to four days to hatch, depending on water temperatures. Eggs and larvae are both found near the surface.

Northern anchovy are subject to intense predation throughout all life stages. Anchovy eggs and larvae fall prey to an assortment of invertebrate and vertebrate planktivores. As juveniles in nearshore areas, anchovies are vulnerable to a variety of predators, including birds and some recreationally and commercially important species of fish. As adults offshore, anchovies are fed upon by numerous marine fishes (some of which have recreational and commercial value), mammals, and birds, including the endangered California brown pelican. A link between brown pelican breeding success and anchovy abundance has been documented.

Northern anchovy eat plankton either by filter feeding or biting, depending on size of the food. Adult anchovy are known to filter anchovy eggs and it is possible that this type of cannibalism is an important factor in regulating population size.

Status of Population

Biomass of northern anchovy in the central subpopulation averaged 440,000 tons during 1964 to 1970, increased rapidly to 2,029,000 tons in 1974 and then declined to 543,000 tons in 1978. Since 1978, biomass levels have tended to decline slowly. Anchovy biomass during 1989 was 338,000 tons.

Maximum sustained yield of northern anchovy in the central subpopulation is estimated to be about 241,000 tons per year at a total biomass level of about 646,000 tons. However this harvest is a long-term average, and annual fluctuations are large.

Although total anchovy harvests and exploitation rates since 1983 have been below the theoretical levels for maximum sustained yield and historical levels, abundance continues to decline slowly. Annual harvests in the near future are expected to be lower because the Mexican reduction fishery has reportedly become unprofitable and has ceased operations. The size of

the anchovy resource is now being determined mostly by natural influences.

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UNDERUTILIZED SPECIES

BOX CRAB

History of the Fishery

While they have rarely been marketed in California, box crabs (*Lopholithodes foraminatus*) have been used commercially in Oregon for several years. The meat, which is found mainly in the claws and legs, is tasty and has good texture, and the meat yield of about 25 percent of the total weight is high compared to that of the more familiar rock crabs. The shell takes on an appealing reddish tinge when cooked, but moderately sharp spines on the carapace and legs detract somewhat from the box crab's marketability. The shell is not as hard as that of rock crabs, however, so the meat is easier to extract.

Box crabs are a common bycatch in the groundfish fisheries of northern California. They are often entangled in gillnets that are used to catch rockfish in deep water, and are also captured, sometimes in large numbers, in trawl nets. Traps used to catch fish or Dungeness crab are also effective for catching box crabs, which are readily attracted to bait. Captured box crabs are usually discarded, or are eaten by fishermen, because of the lack of a market. No regulations apply to the commercial or sport take of box crabs.

An experimental trap fishery for box crab carried out in August and September, 1989, in southern California at the northern Channel Islands, produced only a few crabs. Most of the fishing was conducted in the shallow end of the box crab's range, which may partly account for the poor results. Observations made during that study suggest that long soak times are needed to catch box crab, which may not be as mobile as other crabs and lobsters. In fact it was suggested that trawling may be more efficient than trapping as a means of catching box crabs commercially. Box crabs do poorly in captivity in ambient surface sea water temperatures in southern California; so refrigerated systems are needed in order to keep them alive. On the other hand, they will remain alive out of water for at least two or three days if kept in temperatures under 45°.

The marketability of box crabs was discovered in Oregon in 1983, when El Niño conditions forced fishermen and dealers to look to substitute species for the many normal target species no longer available. Catches jumped from 16,000 pounds in 1983 to 272,000 pounds in 1984, then declined to 93,000 pounds in 1985. Much of the product was sold in the form of picked meat to buyers on the east coast, who needed substitutes for declining resources of "Jonah" crab. The crabs were caught mainly in Dungeness crab pots with entrances made a bit higher to accommodate the shape of box crabs.

Status of Biological Knowledge

When its legs and claws are folded under its body, the box crab resembles an oval rock or, arguably, a small box. Box crabs have a light brown carapace and are white below. The entire front margin of the carapace is armed with short, sharp spines. When the legs are folded inward, a round hole is formed at the

angle of the middle joint between the claw and the first walking leg, from which the scientific name "*foraminatus*" was derived.



Box crab, *Lopholithodes foraminatus*.

In northern California, box crabs are abundant in depths of 300 to 800 feet. Further south, they are more common in somewhat greater depths of about 600 to 1,000 feet. The record depth of capture is 1,800 feet. Box crabs are found on sandy, muddy, and rocky bottom. They may possibly undergo migrations from deep to shallow waters and vice versa during certain seasons.

Little is known about the biology, behavior, or population parameters of this species. Egg-bearing females are common off southern California in February, and hatching probably occurs sometime in spring. Mature males weigh about 1.3 pounds, and the largest individuals are about 2.5 pounds and measure seven inches across the back. Females are smaller than males.

Like other crabs, box crabs probably feed mainly on invertebrates that occur in their habitat. The strong claws are used to grasp and tear their prey into manageable size. The major predator of box crabs is probably octopus. Other animals find it difficult to eat box crabs when they assume their defensive position, with all the appendages folded under the body.

Status of Population

Nothing is known about the abundance of box crabs. Occasional reports of catches of large numbers box crab by trawl fishermen in both northern and southern California suggest that the populations may be sizable. Near San Diego, researchers regularly caught box crabs in baited traps set in depths of 125-175 fathoms. We need to learn more about the life history as well as abundance of box crab in order to determine appropriate catch levels.

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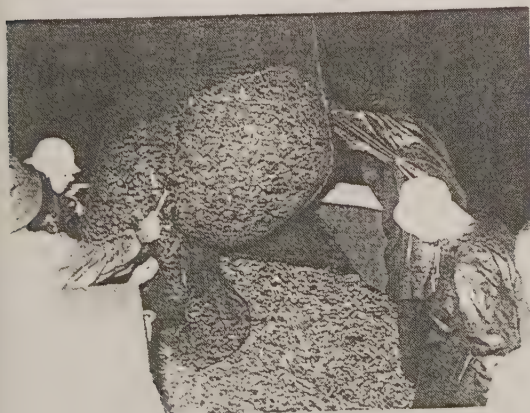
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PELAGIC RED CRAB

History of the Fishery

Pelagic red crabs (*Pleuroncodes planipes*) constitute a large fishery resource when they periodically appear off the southern California coast. The bulk of the resource is centered off southern Baja California, but during warm water years many crabs are carried as far north as Monterey. Although this species is not now fished commercially, in the past it has been used in pet food and aquaculture feed, and other uses have been suggested. The flesh is edible (red crab is closely related to "langostino," which has been imported from Chile for many years), and the shell can be converted to "chitosan," a compound similar to cellulose with a number of practical applications. The carotenoid pigment in red crab can be used to enhance pigmentation in the flesh and skin of fishes, as well as feathers of birds such as captive flamingos. It also gives a desirable golden hue to the skin of chickens.



Midwater trawl catch of pelagic red crabs.

A small fishery for pelagic red crab was initiated in the early 1970's, with practically all of the catches being made off southern Baja California, Mexico. The fishery lasted until around 1977, when extended jurisdiction effectively closed all areas of dense concentration of red crabs to American fishermen. Throughout the fishery's existence, a single boat made all commercial landings of red crabs.

Although large numbers of red crabs are periodically seen off southern California, attempts to catch them in commercial quantities have proven difficult. Thus, the fishery was conducted in southern Baja California, particularly in and near Magdalena Bay. All the landings were made in San Pedro. Initially the crabs were used as an ingredient in canned cat food, but later they were minced and included in the formulation of a salmon feed known as "Oregon Moist Pellets," used extensively by salmon growers. The value of red crab lay in its high concentration of carotenoid pigments which, when ingested and assimilated by salmon, gave the fish flesh its characteristic color. Without the inclusion of carotenoid pigments in the diet, the flesh of cultured salmon is pale.

Both midwater and bottom trawls have been successfully used to catch pelagic red crab. A special problem occurs in unloading the catch from the trawl nets, because the crabs interlock with each other and splitting off manageable amounts in the cod end is difficult. On-board handling and storage are also difficult, because the crabs are light and bulky. Further, enzyme activity quickly causes spoilage. In order to store large quantities aboard a vessel, it was found that grinding and freezing the product in plastic bags was most practical.



Pelagic red crab, *Pleuroncodes planipes*.

Status of Biological Knowledge

The pelagic red crab is a striking red crustacean belonging to the family Galatheidæ, which includes a number of lobster-like crabs. Adult red crabs attain body lengths of only about 2.5 inches, and 100 or more individuals are needed to make up a pound.

Pelagic red crab is normally found off southern Baja California, Mexico, but in years when strong northward transport of water occurs along the west coast it can be found as far north as Monterey. They are found in surface layers, and on the bottom from shallow depths to around 150 fathoms. Although they have been found in temperatures of 48 to 82°, they seem to prefer water temperatures between 59 and 70° F.

Larval and young stages of red crab lead a planktonic life for about a year. In the second year, maturing crabs are about 0.6 inch in carapace length and spend some time on the bottom. By the end of the second year they are slightly larger than one inch long and become strictly benthic.

Red crabs become reproductively mature sometime in their second year. Each female may have two or three broods of eggs in one season, with up to 3,600 eggs in a brood. Eggs hatch about two weeks after they are carried externally. Spawning peaks in the winter, mainly off southern Baja California, but in warm water years spawning can occur as far north as southern California.

Planktonic red crabs feed on phyto- and zooplankton by filtration. Benthic stages probably feed primarily on detritus, but can also feed on dead animal matter and can even catch live copepods by using their chelipeds.

In nature, the red crab is an important food item for many fishes, birds and marine mammals, because of its great abundance and availability. Predators of red crab include most carnivorous fishes, especially tuna off southern Baja California, several species of birds, sea lions and some whales. Off southern California, they constitute an important food item for gulls and probably marine mammals as well, especially during El Niño years when other food such as squid and anchovy are scarce.

Younger stages of pelagic red crab live up to their name, and are transported in all directions by currents from the primary spawning grounds off south-central Baja California. Windrows of these crabs are often seen stretching for miles on and near the surface. Mass strandings of pelagic red crabs occur regularly on beaches in Baja California and periodically happen as far north as Monterey.

Status of Population

Little information is available about the abundance of pelagic red crab. One survey by a Russian research vessel found around 300,000 tons of red crabs in an area of 77,000 square miles off Baja California. In another study, stomach contents of tunas caught in this area indicated that the fish ate around a pint of red crabs daily; so the total abundance must be considerable. Off California, however, large quantities occur only infrequently, when warm currents carry the crabs northward from the center of abundance off Baja California.

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SPOTTED RATFISH

History of the Fishery

The spotted ratfish or chimacra (*Hydrolagus collieri*) is presently not used commercially in California, and probably is eaten only rarely on the occasions when it is caught by recreational fishermen. However, fillets of chimacra have recently been imported into California, probably from Argentina and Chile, and have been sold in restaurants as well as fish markets. Chimacras, called "ghostsharks" in New Zealand where the fillets are sometimes marketed as "pearl fillets," have been eaten there as well as in South Africa for many years. Chimacras are also used as food in China, but no information is available on the amount consumed. The large liver also yields an all-purpose oil of good quality, which has been used as an

external and internal medication as well as a lubricant. Spotted ratfish is commonly taken in trawl nets, and may represent a sizable underutilized resource in California. Total world landings are on the order of 3,000-4,000 tons annually, primarily in New Zealand, Chile, and Argentina.

Spotted ratfish are commonly found in the bycatch of bottom trawl nets. They are also caught by baited hooks that are fished near or on the bottom, and in bottom set gill nets.



Spotted ratfish or chimacra, *Hydrolagus coliei*.

Status of Biological Knowledge

The spotted ratfish is an extraordinary fish, with a silvery to bronze body dotted with numerous white spots, and a smooth, scaleless skin often having a metallic cast. Large green eyes are set in a head that resembles that of a rabbit. The strong dorsal spine contains a venom which, though not lethal, can cause severe pain. Chimacras are similar to sharks in having a cartilaginous rather than bony skeleton.

Found from western Alaska to the tip of Baja California, and in the northern part of the Gulf of California, it is common in depths from 1,000 to 1,300 feet in spring. It is a bottom dweller, and occurs in shallow waters in the northern extremes of its range, but has been found as deep as 3,000 feet.

Studies which use marks on vertebrae and spines have not been successful in estimating the age of ratfish, nor have those which use eye lens weights and body length modes. Females apparently grow to a larger size than males. In one collection of 448 ratfish, no males were as long as 20.4 inches, while ten females were between 20.4 and 21 inches. The largest recorded length is 38 inches.

Some females are mature at a length of 18 inches, while all are mature by the time they are 20 inches long. Fertilization is internal. Males have two hooked clasping organs in front of the pelvic fins and, like male sharks, are equipped with a pair of claspers which are used to transfer sperm capsules into females.

The female lays leathery egg cases which are five to six inches long and are wide at one end and narrowly tapered at the other, which sticks into the mud bottom. Egg-laying usually occurs in spring and summer, but some females and most males are reproductively active throughout the year. Egg capsules are probably laid in pairs, and it is possible that fertilization of a second pair of eggs may follow soon after the first pair is released, and that those are released soon thereafter.

The teeth of ratfish are arranged in three pairs of large flat plates, two pairs in the upper jaw and one pair in the lower. Feeding habits reflect an opportunistic nature, and the diet includes clams, snails, shrimps, nudibranchs, annelid and polychaete worms, coelenterates, amphipods, small fishes, and

heart urchins. Many large fishes such as lingcod, rockfish, and halibut, as well as several species of sharks and marine mammals, probably eat ratfish.

Spotted ratfish in the Gulf of California apparently migrate seasonally, but this may be due to special hydrographic conditions within the Gulf and may not be indicative of distribution patterns elsewhere.

Status of Population

Nothing is known about the size of the population of spotted ratfish. The species has never been purposely sought in California, but is caught regularly by fishermen targeting other species. Spotted ratfish are common in relatively shallow smooth bottom grounds where trawlers work, and are also found in rocky areas. Since they are not gregarious, it is rare to catch them in large numbers. Fecundity is low and, like sharks, chimacras are probably more susceptible to overfishing than are bony fishes, which produce a large number of offspring.

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PACIFIC SAURY

History of the Fishery

In California, interest in fishing Pacific saury (*Cololabis saira*) was initiated in the 1950's, when the decline in abundance of Pacific sardine caused fishermen and processors to look for substitute species which could be used to make fish meal. Sporadic landings of saury were made in San Pedro, where the fish were reduced into oil and meal. In the late 1960's and early 1970's, Japan, the Soviet Union, and the U.S. became interested in harvesting saury off the U.S. west coast because western Pacific stocks had fallen to all-time low levels.

Fishing trials by U.S. researchers and fishermen were conducted north of Monterey, where larger saury were more common. Most of these trials, which involved the use of purse seines and a Japanese fishing method using light attraction together with a type of blanket net (called *bo-uke ami*), were largely unsuccessful. Japanese saury fishing vessels which fished off the west coast around the same time were a little more successful. From 1969 through 1972 they caught 507, 3,600, 1,430, and 77 tons. Japanese vessels were larger than those of the U.S., and used attracting lamps with 50 kilowatts of power. Catches per unit of effort were not considered high enough for economical fishing, however. Rough seas off the Oregon and

Washington coasts, and scarcity of dense concentrations of large saury, were blamed for the low catch rate. The fish averaged just eight to nine inches in length and had a low oil content.

After western Pacific stocks rebounded in the mid-1970's, efforts to harvest saury here were discontinued. Because of its large biomass and good eating qualities, the saury resource will likely be utilized some day off California and elsewhere in the eastern Pacific. However, economics of fishing, handling, and processing, coupled with the present lack of a domestic market make fishery development doubtful in the near term. Export as a food product is also unlikely, because of the large catches in the western Pacific and because the Japanese prefer their own fish, which appear to have a higher fat content. Externally attached copepods also detract from the appearance of eastern Pacific saury.



Pacific saury, *Cololabis saira*.

Status of Biological Knowledge

Pacific saury are slender, silvery fish common throughout the entire temperate north Pacific Ocean. They grow to about 12-13 inches "knob length," the distance from the tip of the lower jaw to the muscular knob at the base of the tail fin (approximately 94% total length). The flesh of saury is firm and rather oily. The fish is widely used in Japan, where it is sold in fresh, frozen, dried, and canned form. The meat yield is around 60 percent, and the oil content varies from three to 10 percent. In addition to its use as food and fish meal, saury is a preferred baitfish in the longline fishery for tuna.

Pacific saury are found in a broad band across the Pacific Ocean, from around 20-25° north latitude to the Gulf of Alaska. Within this broad area, three groups of saury are distinguishable: one in the eastern Pacific, the second in the central Pacific and the major group in the western Pacific. Off the U.S. west coast, saury occur from near shore to perhaps 300 miles offshore, but are most common from 40-100 miles off the coast.

Young fish appear to remain in California waters, while older fish migrate to the north, probably to the southern Gulf of Alaska, when coastal waters warm up in summer. As the water cools in fall and winter, saury again move south to preferred temperatures off California. One study found mean lengths of 7.9, 9.3, and 10.9 inches for saury from California, Oregon, and Washington. No fish greater than 12 inches were found off California and, conversely, all fish caught off Washington were larger than seven inches. Optimum temperature range for saury off California is 57-63° F.

During the day saury are usually found in depths of 100-230 feet, where they feed, but have been found as deep as 750 feet. At night, they usually swim near the surface and are attracted to light. Large numbers often accumulate under the lights of stationary or slow-moving vessels. Fish over 11 inches show poor attraction to light, however, especially during

spawning periods. In California, fishing for adult saury is apt to be most successful in the fall, north of San Francisco, and from 40-120 miles offshore.

Growth rate and longevity of Pacific saury have been subjects of controversy for many years. Interpretations of growth marks on scales and otoliths, as well as results derived from analyses of sizes of fish caught by commercial fisheries, have produced conflicting hypotheses. Various earlier workers in Japan and the Soviet Union felt that western Pacific saury had a life span of three to six years, and that saury were capable of spawning at age two. Females were thought to spawn three times a year, releasing 500 to 2,000 eggs, or perhaps as many as 5,000 eggs depending on their size, during each spawning episode, in a season of around seven months starting in late August. Later Japanese studies indicated that two major groups existed, one spawning in spring and the other in autumn, and that the probable life span was two or two and a half years. More recent studies involving daily growth rings on saury otoliths suggest that most saury in the western Pacific live for only a year, while some may reach two years of age. Fish around 11.4 inches, which are commonly caught in the Japanese commercial fishery, are thought to be nearly a year old. Fish over 12.6 inches, relatively scarce in the catch, may be 1.5 to two years old. Examination of otoliths of larval and early juvenile saury grown from eggs in tanks showed that the growth rings were indeed laid down daily, at least for the first month.

Daily growth rings found on the otoliths of eastern Pacific saury suggest that the growth rate is considerably lower than that of fish from the western Pacific. By the end of the first year, eastern Pacific saury are thought to grow to nine inches, while western Pacific fish attain 12 inches. Some researchers think, however, that eastern Pacific saury reach a length of only 6.5 inches at the end of the first year, and are about 10.6 inches at the end of the fourth year. The largest fish are about 13.4 inches and 6.5 ounces. Fish of this size are rare, and only a few are thought to survive beyond age five. Sexual maturity occurs during the second year, when the fish are around 7.9 inches. Fecundity was estimated at 1,600 eggs for a female of 10 inches, for each of three spawning episodes in a season. Spring- and autumn-born groups were also identified in the eastern Pacific, with the former predominating in fish sampled from California to Washington. Studies on genetics of the two spawning groups revealed no differences.

Spawning occurs primarily in spring off California, and in August, October, and winter off Washington. In California, the highest number of eggs was found in the plankton from Morro Bay to San Diego, mostly from April through June. Although saury spawn at all hours, peak number of eggs are found around midnight, early morning, and mid-afternoon. Eggs normally attach to each other and to floating objects by means of filamentous threads. The larvae hatch out in 10 days at 68° F, and 17 days at 58° F, and are usually found just under the water surface. Juveniles can be found down to depths of 80 feet. Prevailing currents in southern California disperse some larvae to the west as well as northward, but most remain near the spawning grounds.

Pacific saury feed on small zooplankton, particularly copepods, euphausiids, crab megalops, and other small crustaceans.

Yellowtail, bluefin and albacore tuna, and striped marlin are major predators of saury, as are fur seals, sei whales, some birds and squid.

Status of Population

Although there is some disagreement among researchers, it is generally thought that the eastern and western stocks do not mix, while the central stock mixes with the western and perhaps also to a lesser degree with the eastern Pacific stock. Genetic studies of western saury stocks indicate that they are comprised of perhaps four subpopulations, but exchanges of genes often occur among the groups.

The western and central stocks appear to be indistinguishable genetically; so mixing may be considerable. The eastern Pacific stock may provide recruits to the central area also. Rather large differences in growth rate and longevity suggest that eastern and western Pacific stocks, however, are isolated.

Recent estimates of population size of eastern Pacific stocks of saury are unavailable. In the past, surveys by research vessels showed that the number of eggs and larvae, and by extension the spawning populations, of saury off Mexico and California fluctuated considerably through the years. The estimated quantity of adult saury in the area between central Baja California and San Francisco ranged from 97,000 to 294,000 tons per year, averaging 200,000 tons, between 1950 and 1966. The size of the total population in the northeastern Pacific is probably on the order of 450,000 tons. An annual limit of around 33,000 tons of adult saury, half of the estimated maximum sustainable yield, has been suggested for the entire west coast stocks, including Canada.

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landings of whitefish were made in 1926, when 368,000 pounds were recorded in southern California. Some of these fish may have been caught off Baja California. Landings since then have declined, but the value of ocean whitefish catch almost tripled from 1978 to 1989.

Annual catches made from commercial passenger fishing vessels ranged from 22,000 to 84,000 fish from 1977 through 1989. Most of these fish were caught near the Channel Islands and at offshore banks, particularly Cortez and Tanner Banks near San Clemente Island. They are caught exclusively with baited hooks, and no special fishing regulations pertain to their catch. The vicinity of the Coronados Islands off Mexico is a favorite whitefish fishing area for sport fishermen.

It is a food fish favored by sportsmen, and the small amount of ocean whitefish that is landed commercially is sold in fresh fish markets. It makes excellent sashimi, being comparable in flavor and texture to any of the most esteemed white-fleshed fish used for this purpose. In Japan, species of tilefish similar to ocean whitefish command premium prices in the fresh fish market. In fact, several years ago, two longline fishing vessels were sent from Japan to fish for ocean whitefish at offshore banks near southern Baja California. Unfortunately, here in California ocean whitefish has acquired a mixed reputation because a few bitter-tasting individuals turn up every now and then. The cause of the bitter flesh is unknown, but these fish are evidently restricted to shallow waters, especially near kelp beds. Smaller individuals make excellent aquarium pets, as they are hardy, handsome, active, and alert when placed in tanks.



Ocean whitefish, *Caulolatilus princeps*.

Status of Biological Knowledge

Ocean whitefish are attractive fish with robust, elongate bodies. They are white below and light brown on the back, with fins marked with blue and yellow streaks and yellow margins.

The range of ocean whitefish is from Vancouver, British Columbia to Peru or possibly to Antofagasta, Chile, and the vicinity of the Galapagos Islands. In California, it is common south of Pt. Conception and rare to the north. Its depth range is 30–450 feet, and its principal habitats appear to be near offshore islands and over shallow banks, at depths of 50–150 feet.

The southern California population of ocean whitefish is derived from central and southern Baja California. No information is available on the timing or the size at which most of these fish migrate northward. It is also not known if the fish move south again to spawn, or if any spawning occurs off California.

Fish close to spawning have been found in Baja California from October through April. Most larvae occur within 100

OCEAN WHITEFISH

History of the Fishery

Ocean whitefish (*Caulolatilus princeps*), is a popular sport fish in southern California, is also a commercial species, but landings in recent years have been rather low. The greatest

miles of the central Baja California coast. These larvae are found throughout the year, but their numbers peak in summer. Pelagic juvenile stages barely one-half inch long have been found far offshore from Baja California. Juveniles move inshore by the time the fish reach 2.5 inches or so. At an age of six years whitefish are 20-21 inches long and weigh three to four pounds, while at age 13, which is about their life span, they average around 25 inches and 7.5 pounds. Ocean whitefish may grow to a maximum of 40 inches and 12 pounds.

Ocean whitefish have a relatively small mouth, and accordingly they feed upon small animals, including shrimps, crabs, pelagic red crab, octopi, squid, and various fishes, especially anchovy and lanternfish. They are usually encountered over rocky grounds, and anglers find that they usually take baited hooks before the lures reach bottom.

Young ocean whitefish are eaten by a number of fishes, including albacore tuna. Older stages are prey for giant sea bass, sharks, and no doubt other large fishes. Otoliths (earbones) of whitefish found in middens at San Clemente Island attest that this fish was an important food fish for Native Americans.

Status of Population

Because the center of distribution of ocean whitefish is far to the south off central Baja California, the numbers of ocean whitefish near southern California have never been very high. The decrease in commercial landings after the mid-1940's may not reflect reduction in availability or abundance of ocean whitefish, but rather a disinterest by the market. No information is available on the size of the populations, either in southern California or in Mexico.

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in Taiwan the intestines bring over \$11.00 per pound. The flesh of ocean sunfish has at times been reported to be toxic, but a thorough review and investigation of such reports disclose no authenticated case of poisoning from eating it. On the contrary, it is considered delectable by those that eat it. Since the flesh is somewhat watery, it is better to parboil the meat to remove some moisture. The meat then becomes firm, and the texture similar to that of shellfish. The flesh is sometimes infested with long string-like parasites, but these can be easily removed and, in any case, are not harmful when ingested. Another negative attribute is the low yield of meat found in sunfish. Because the skin and cartilaginous skeleton are so heavy, only about 20 percent of the weight of the fish is edible flesh.

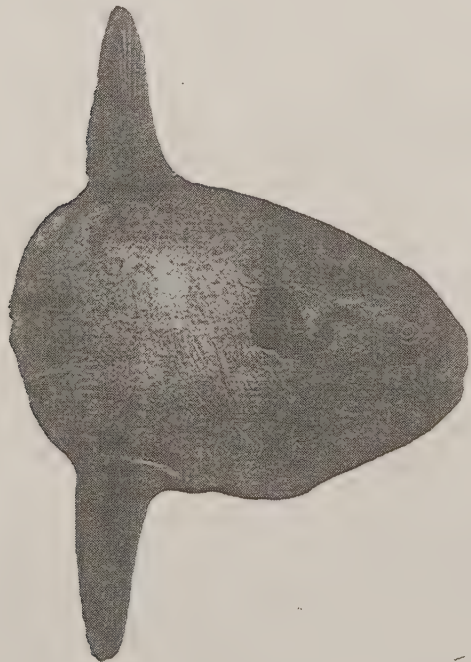
Only a few ocean sunfish are brought in by fishermen for food, and very little reaches the fish market. The fish are often caught in drift gillnets which target swordfish and sharks. At times as many as 200 sunfish are caught in a mile-long net, but nearly all the fish are released alive by the fishermen. Some sunfish are also caught incidentally in roundhaul nets together with mackerel, anchovy, or sardine. Most incidental catches of ocean sunfish are made in southern California, but at times drift gillnetters also catch substantial numbers between San Francisco and Pt. Conception. Roundhaul net catches are also made primarily in southern California, but the small wetfish fleet in Monterey also captures some sunfish. A few sunfish are also caught on hook and line, as well as with harpoons. No fishing restrictions apply to ocean sunfish.

OCEAN SUNFISH

History of the Fishery

The ocean sunfish (*Mola mola*) is presently not sought by most commercial or sport fishermen here. However, a few fishermen who have learned from Mediterranean or Asian counterparts about its excellent eating quality consider it a delicacy. In Japan the liver is also used as a condiment for sunfish meat sashimi, and in Taiwan the intestine is the most expensive part of the fish.

Ocean sunfish is not sold here, but wholesale prices in Japan for the meat and liver are well over \$5.00 per pound, and



Ocean sunfish, *Mola mola*.

Status of Biological Knowledge

The ocean sunfish is a peculiar looking fish, with a truncated body and no tail. Its silvery body is oval and compressed, with tall slender fins sticking out near the posterior end. Its skin is leathery, and underlined with a thick layer of heavy cartilage. Ocean sunfish are found in most temperate and warm seas of the world. Most sightings of this fish in California are from south of Point Conception during winter and spring, and from there to San Francisco in summer and early fall. Ocean sunfish are usually observed swimming casually on the surface, with their long dorsal fin sticking high up in the air, but they are also sometimes seen lying on their side at the surface. Sunfish no doubt also occur in midwater, wherever food organisms are abundant.

Little is known about the natural history of ocean sunfish. Most sunfish caught in driftnets in southern California are under two feet long and less than 20 pounds, but larger individuals to 100 pounds or more are not uncommon. The largest individuals reported in the literature were estimated to have been over 10 feet long and nearly as wide between the tips of dorsal and anal fins, and weighing perhaps as much as 3,000 pounds.

Spawning grounds have been found in the northwestern Pacific Ocean, at around 30° N latitude and 130° E longitude. One large female of about 4.5 feet was estimated to have had 300 million eggs, although not all of those would be laid at one time. A few planktonic post-larvae of sunfish have been found on the high seas, but fertilized eggs or early larval stages are absent from plankton collections. The shape of young larvae is similar to that of other fishes, but the sunfish larva soon loses its tail and acquires a number of long spike-like projections all over the body.

The ocean sunfish has a small mouth and its teeth are fused into a sharp-edged plate in both the upper and lower jaw. It usually eats small crustaceans, fish, mollusks, jellyfish and other soft-bodied forms that are found near the ocean surface. Larger fish have also been found in their stomachs at times. The

long intestine of ocean sunfish is reminiscent of algae eaters, and indeed seaweed has also been found in their stomachs. Sharks and sea lions are the major predators of ocean sunfish.

Occasionally they are seen on the surface hovering patiently while seabirds peck on their tough hides, apparently picking off external parasites. They also have been observed by divers being "cleaned" of these parasites by small fishes which do this service for many species of fish. Ocean sunfish have frequently been seen leaping high in the air, though it's hard to imagine how they can find enough momentum without the aid of a tail fin. Mass mortalities of small ocean sunfish have occurred from August through October in Monterey Bay, where dozens of the silvery fish have been found dead on the shallow bay floor or floating on the surface. No explanations have been offered for such mass deaths.

Status of Population

Nothing is known about the population size or structure of ocean sunfish. Since they occur throughout most temperate and warm seas, it is possible that all ocean sunfish are part of a single population, at least in the Pacific Ocean. In California, those that are caught are usually returned to the ocean alive by gillnetters and, since there is no directed fishery for them, abundance of ocean sunfish here is probably rather uniform from year to year. The effect of mass mortalities is unknown, but they no doubt cause lowered population levels in localized areas.

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Cardiac physiology in tunas. II. Effect of ryanodine, calcium, and adrenaline on force–frequency relationships in atrial strips from skipjack tuna, *Katsuwonus pelamis*

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Force–frequency relationships and the dependence upon extracellular calcium as a source of activator calcium were investigated using atrial strips from the skipjack tuna (*Katsuwonus pelamis*). At 25°C, active force generation increased over a stimulation range of 0.2–1.6 Hz and declined at higher stimulation frequencies. Ryanodine, a blocker of calcium release from the sarcoplasmic reticulum, decreased active force by ~30% but did not alter the shape of the force–frequency curve. Uniform contractions were maintained up to stimulation rates of 3.0 Hz following ryanodine application, compared with 3.4 Hz under control conditions. Active force increased with increasing extracellular calcium concentration in a concentration-dependent manner with greatest sensitivity over the range of 1.0–5.0 mM calcium. Activation duration decreased with increasing extracellular calcium concentrations up to 5.0 mM and with increasing contraction frequency up to 1.0 Hz. Relaxation duration also was reduced with increasing extracellular calcium over a range of 0.5–4.0 mM, and over a stimulation range of 0.2–0.6 Hz. Adrenaline increased active force threefold over the range of 10^{-8} to 10^{-5} M, with an EC_{50} value of $4.90 \pm 0.57 \times 10^{-7}$ M. The EC_{50} value was not dependent upon stimulation frequency. These results indicate that contraction in the skipjack tuna atrium is partially dependent upon intracellular calcium release from the sarcoplasmic reticulum. In this manner, the tuna heart more closely resembles the mammalian model of excitation–contraction coupling than that suggested for other fishes in which activator calcium is almost exclusively derived from extracellular influx.

KEEN, J. E., FARRELL, A. P., TIBBITS, G. F., et BRILL, R. W. 1992. Cardiac physiology in tunas. II. Effect of ryanodine, calcium, and adrenaline on force–frequency relationships in atrial strips from skipjack tuna, *Katsuwonus pelamis*. Can. J. Zool. 70: 1211–1217.

Les relations force–fréquence et le rôle du calcium extracellulaire comme source de calcium d'activation ont été mesurés sur des bandes de tissu d'oreillette chez le Thon à ventre rayé, (*Katsuwonus pelamis*). À 25°C, la production d'une force active augmente entre les fréquences 0,2 et 1,6 Hz, mais diminue aux fréquences de stimulation plus élevées. La ryanodine, un inhibiteur de la libération du calcium dans le réticulum sarcoplasmique, diminue la force active d'environ 30%, mais ne modifie pas la forme de la courbe force–fréquence. Des contractions uniformes sont obtenues par l'application de taux de stimulation allant jusqu'à 3,0 Hz après l'application de ryanodine; cette valeur atteint 3,4 Hz dans des conditions témoins. La force active augmente en fonction de la concentration de calcium extracellulaire selon une relation de dépendance et la sensibilité est maximale entre 1,0–5,0 mM de calcium. La durée de l'activation est fonction inverse de la concentration de calcium extracellulaire jusqu'à concurrence de 5,0 mM et de la fréquence de la contraction jusqu'à 1,0 Hz. La durée de la relaxation diminue aussi lors d'une augmentation de calcium extracellulaire aux concentrations situées entre 0,5 et 4,0 mM et d'une augmentation de la stimulation dans l'étendue 0,2 à 0,6 Hz. L'adrénaline augmente la force active par un facteur de 3 dans l'étendue 10^{-8} à 10^{-5} M et la valeur du EC_{50} est de $4,90 \pm 0,57 \times 10^{-7}$ M. La valeur du EC_{50} est indépendante de la fréquence de stimulation. Ces résultats indiquent que la contraction de l'oreillette du Thon à ventre rayé est partiellement dépendante de la libération de calcium intracellulaire provenant du réticulum sarcoplasmique. Sous cet aspect, le cœur d'un thon ressemble donc plus au modèle de couplage excitation–contraction d'un mammifère qu'au modèle suggéré pour d'autres poissons dans lequel le calcium d'activation provient surtout d'un apport extracellulaire.

[Traduit par la rédaction]

Introduction

Tuna are the most athletic of any fish species and have cardiac features on a par with many mammals of equivalent size. Cardiac output ($132 \text{ mL} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) in spinally blocked skipjack tuna (*Katsuwonus pelamis*) (Bushnell 1988) compares more favorably with estimates in mammals (dog, $103 \text{ mL} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$, Liang and Huckabee 1973; rabbit, $193\text{--}300 \text{ mL} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$, White *et al.* 1974) than in other fishes (Atlantic cod (*Gadus morhua*), $17.3 \text{ mL} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$, Axelsson *et al.* 1986; rainbow trout (*Oncorhynchus mykiss*),

$17.6 \text{ mL} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$, Kiceniuk and Jones 1977). Similarly, regulation of cardiac output has been suggested to be primarily mediated through control of heart rate (Farrell *et al.* 1992), as in mammals, rather than through major modifications in stroke volume, as in other fishes (Farrell 1991). In fact, the high heart rate is one of the more striking differences between the tuna and most other lower vertebrates. In most lower vertebrates examined so far (fishes, amphibians, and reptiles), heart rate does not exceed 120 beats per minute (bpm; Farrell 1991). Tuna, on the other hand, have heart rates more like

those of small mammals than fish. In spinally blocked skipjack tuna, resting heart rates may average 120 bpm (117 ± 12 bpm; Bushnell *et al.* 1990), and maximal rates from swimming tuna have been measured to be greater than 200 bpm (Kanwisher *et al.* 1974; Brill 1987). The maintenance of a high heart rate is dependent upon appropriate activation and relaxation mechanisms. The former, at least, appears to be different in upper and lower vertebrates.

Mammalian cardiac excitation-contraction (E-C) coupling is considered to involve a small influx of calcium across the sarcolemma through voltage-dependent channels, which acts as a trigger for a greater release of stored calcium from the sarcoplasmic reticulum (SR). The intracellularly stored calcium is the primary activator of contractile processes (Fabiato 1983). Lower vertebrates, however, appear to have a greater reliance on extracellular calcium for direct activation of myofilaments. Although well-developed (Page and Niedergerke 1972; Santer 1974), the SR is comparatively sparse, by mammalian standards. Furthermore, the magnitude of extracellular calcium influx has been demonstrated in frog (Morad and Cleeman 1987) and suggested in fish (Vornanen 1989; Tibbitts *et al.* 1991) to be sufficient to support myocyte contraction. Given the high heart rate found in tuna, it was of interest to determine the relative contribution of extra- and intra-cellular calcium to contractile function in tuna heart, i.e., whether E-C coupling in the tuna heart more closely resembles the pattern found in higher or lower vertebrates. This study examines the response of skipjack tuna atrial strips to agents affecting intracellular calcium concentration.

Materials and methods

Twelve skipjack tuna (1.39 ± 0.06 kg) were purchased from local fishermen and held in outdoor tanks ($24-26^\circ\text{C}$) at the Kewalo Research Facility (Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Hawaii).

Tuna were stunned by a sharp blow to the head, and the heart was quickly excised and placed in an ice-cooled modified Cortland saline (pH 7.8 at 25°C) of the following composition (in mM): NaCl, 185.7; KCl, 7.0; $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$, 1.9; $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, 1.1; *N*-tris[hydroxymethyl]methyl-2-aminoethanesulfonic acid (TES, Na salt), TES (free acid), 2.8; dextrose, 5.5. This saline was used throughout all experiments except when calcium was changed as an experimental variable. All chemicals were reagent grade and were purchased from Sigma (St. Louis, Missouri) with the exception of ryanodine, which was purchased through Calbiochem (San Diego, California). Atrial strips were dissected using two parallel razor blades. Thin (5-10) silk threads were tied to both ends of the strip, which was mounted in a saline-filled, O_2 -aerated and water-jacketed (25°C) organ bath (20 mL volume). One end was attached to a fixed post and the other to a Metrigram isometric force transducer (Gould, Cleveland, Ohio). Signals from the force transducer were suitably amplified and displayed on either a 220 or 8000S Analog chart recorder (Gould, Cleveland, Ohio). Strips were electrically paced by a Grass SD9 Student stimulator delivering current via two flattened platinum electrodes positioned on both sides of the strip. The voltage was 1.25 times the threshold required to produce a contraction (22.6 ± 1.4 V) and pulse duration was 10 ms. Muscle strips were stretched until active force (generated force) reached a peak and were allowed to equilibrate for 1 h at a basal stimulation rate of 1.0 Hz. Strips were discarded if passive force exceeded 30% of total generated force at this frequency. Bath saline was then replaced with fresh saline and, following an equilibration period, the strips were exposed to one of the three following protocols.

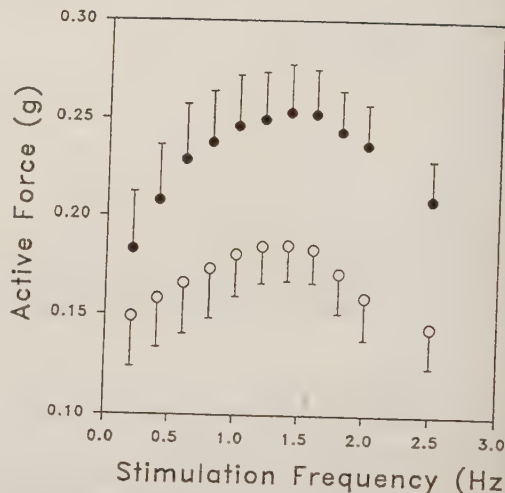


Fig. 1. Changes in peak force generation by atrial strips from skipjack tuna with stimulation frequency, in the absence (●) and presence (○) of $10 \mu\text{M}$ ryanodine. Pairwise comparisons of rate-dependent values were found to be significantly different in all cases ($p < 0.05$). Values are given as means $\pm$ SE or $-$ SE. $N = 5$.

Protocol 1

Stimulation frequency was changed to 0.2 Hz and increased stepwise (0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.0, 2.5, 3.0, 3.5, 4.0 Hz) until contractions displayed nonuniform twitches. At the conclusion of the trial, the control stimulation frequency (1.0 Hz) was reestablished. To examine the relative contribution of the SR to force development, ryanodine, a blocker of SR calcium release, was applied to a final concentration of $10 \mu\text{M}$ (Sutko and Kenyon 1983). The atrial strip was stimulated for 30 min after which the force-frequency trial was repeated.

Protocol 2

The dependency of force generation on extracellular calcium (Ca_o^{2+}) was examined over a calcium range of 0.5–10.0 mM Ca_o^{2+} and stimulation frequency range of 0.2–2.5 Hz. Bath saline was changed from control saline (1.9 mM Ca_o^{2+}) to one containing 0.5 mM Ca_o^{2+} . After equilibration at 1.0 Hz, stimulation frequency was changed to an initial test frequency of 0.2 Hz and the strip allowed to reequilibrate (1–2 min). Calcium concentration was then increased by sequential addition of a volume of saline-based stock calcium chloride solution. Following the test of the highest calcium concentration (10.0 mM), the bathing solution was replaced with the control saline (1.9 mM Ca_o^{2+}) and the muscle strip paced at the control stimulation frequency of 1.0 Hz. The bath solution was changed twice over a 10 min period to ensure complete return to control calcium levels; following equilibration, the atrial strip was reexposed to 0.5 mM Ca_o^{2+} saline and the protocol repeated at a new test frequency (0.4–2.5 Hz).

Protocol 3

The influence of adrenaline, an adrenergic agonist that operates, in part, through modifying the influx of Ca_o^{2+} , was examined through concentration-response curves generated at different test frequencies. Upon reaching steady-state force generation in control saline, stimulation frequency was changed from 1.0 Hz to a test rate (0.2–2.5 Hz). After equilibration, sequential addition of stock adrenaline produced a range of adrenaline concentrations from 10^{-10} to 10^{-4} M. Total added volume after final adrenaline application (at 10^{-4} M adrenaline) was 1.6% of the initial bath volume. After completion of the dose-response trial, the control stimulation frequency (1.0 Hz) was reimposed and the bath solution changed twice over a 10-min period.

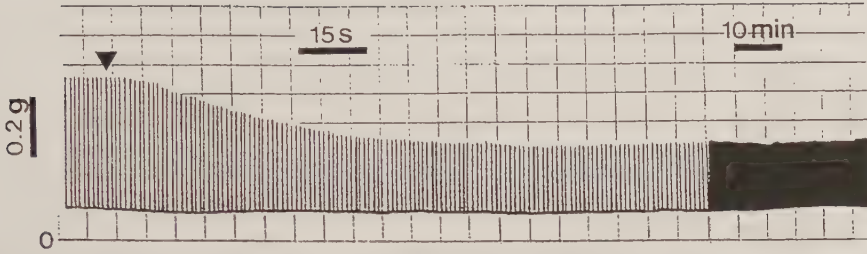


FIG. 2. Effect of ryanodine on force generation in atrial strips from skipjack tuna. The atrial strip was stimulated at 1.0 Hz in control saline. Ryanodine ($10 \mu\text{M}$) was added at the arrowhead. Time (in seconds and minutes) is indicated on the abscissa and force (in grams) on the ordinate.

At least 20 min (total time) was given between the return to control rate and the next test rate to ensure return of the muscle strip to a pre-adrenaline exposure condition and to minimize potential adrenoceptor desensitization phenomena.

After each manipulation the trace was run at a faster chart speed to estimate the time from 50% peak to peak force (activation duration) and the time from peak force to 50% of generated force (relaxation duration).

Muscle strips were weighed and the lengths measured using a micrometer and dissecting microscope. Widths were estimated assuming a specific gravity of $1.06 \text{ g} \cdot \text{cm}^{-3}$ and that the atrial strips approximated a cylinder. Mean length was 6.2 mm (range 3.9–7.8) and width estimates averaged 0.8 mm (range 0.6–0.9). As it is difficult to assess the number of dead or damaged fibers in muscle strip preparations, measurements are not presented per unit fiber weight or cross-sectional surface area.

Statistics were performed using paired and unpaired Student's *t*-tests where appropriate. A significance level of 0.05 was used in all instances.

Results

Force–frequency trials revealed active force generation to be biphasic (Fig. 1). Active force development increased with increasing stimulation frequency, with peak force (F_{max}) being developed at 1.4–1.6 Hz. Force generation declined at higher test frequencies. Following administration of ryanodine ($10 \mu\text{M}$), tension development quickly declined (Fig. 2) and a new steady state was essentially reached after 5 min of exposure. Rate trials were repeated after 30 min of exposure to ensure complete equilibration of ryanodine with the fibers. Ryanodine treatment (30 min incubation) significantly ($p < 0.05$) reduced active force production by $\sim 30\%$ at frequencies generating peak force (Fig. 1). Active force over this same time period in unexposed fibers was typically reduced by $< 5\%$ of initial values. The decline in force in ryanodine-treated strips contrasts with previous studies (Driedzic and Gesser 1988) using ventricular strips from Atlantic cod and sea raven (*Hemirhamphus americanus*), in which active force generation was not significantly modified by ryanodine.

The biphasic nature of the force–frequency curve was essentially unchanged by ryanodine application (Fig. 1). While not significantly affected ($p > 0.05$), the slope of the ascending arm of the curve was somewhat reduced, and this was reflected by a greater relative increase in F_{max} as a function of force generated at 0.2 Hz prior to ryanodine addition (48%, before; 37%, after). Passive force was unchanged following ryanodine application. Ryanodine also significantly ($p < 0.05$) depressed the maximal stimulation frequency generating uniform contractions (SF_{max} ; not shown), from $3.4 \pm 0.3 \text{ Hz}$

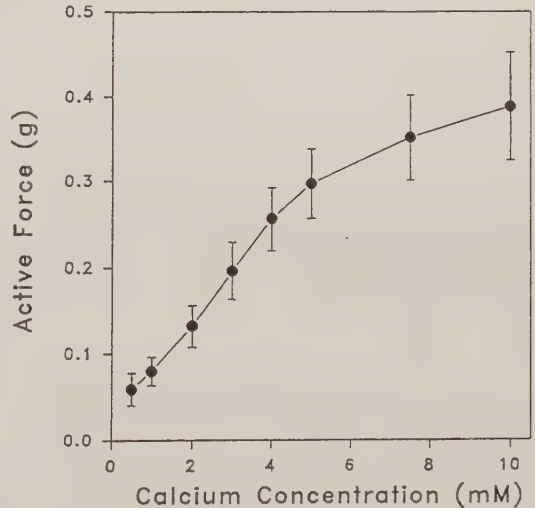


FIG. 3. Active force development as a function of external calcium concentration in atrial strips from skipjack tuna. Stimulation frequency did not have an effect on the slope (not shown). The depicted plot is from trials with a stimulation frequency of 0.2 Hz. Values are given as means $\pm$ SE. $N = 6$.

(control) to $3.0 \pm 0.2 \text{ Hz}$ (ryanodine). Control SF_{max} values are in good agreement with *in vivo* estimates: swimming tuna have maximal heart rates of 180–210 bpm (3.0–3.5 Hz) (Brill and Bushnell 1991).

Active force generation increased with increased calcium concentration in the bathing solution (Fig. 3). Passive force was not significantly changed ($p > 0.05$). The “ Ca_0^{2+} -response” curve was not altered by changes in stimulation frequency. The concentration producing half-maximal force development (EC_{50}) was similar at all stimulation rates and averaged $4.1 \pm 0.2 \text{ mM}$ Ca_0^{2+} . The slope of force development was greatest over the range of 1.0–5.0 mM Ca_0^{2+} . At the highest Ca_0^{2+} concentration (10.0 mM) force was, on average, 8.7 times greater than that at the lowest Ca_0^{2+} concentration (0.5 mM). At a stimulation rate of 0.2 Hz (Fig. 3), active force generation increased by an estimated 90% over the range of 3–9 mM. The sensitivity of skipjack tuna atrial strips to changes in Ca_0^{2+} is thus relatively greater than that found by Driedzic and Gesser (1988) for ventricular strips of spiny dogfish (*Squalus acanthias*,

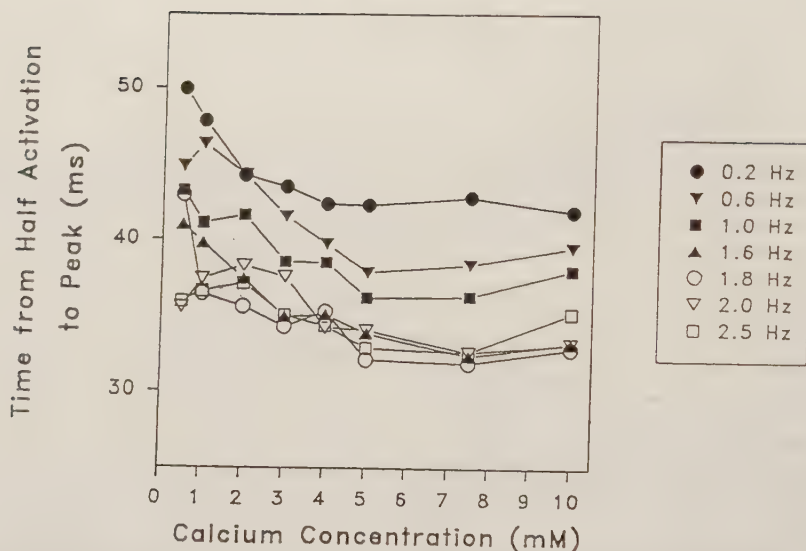


FIG. 4. Activation time (time from 50% of peak to peak force) as a function of extracellular calcium concentration and stimulation frequency (see legend) in atrial strips from skipjack tuna. Each point is the mean of six values. The SE (not shown for purposes of clarity) averaged less than 5% (range 1.6–9.6%) of the mean.

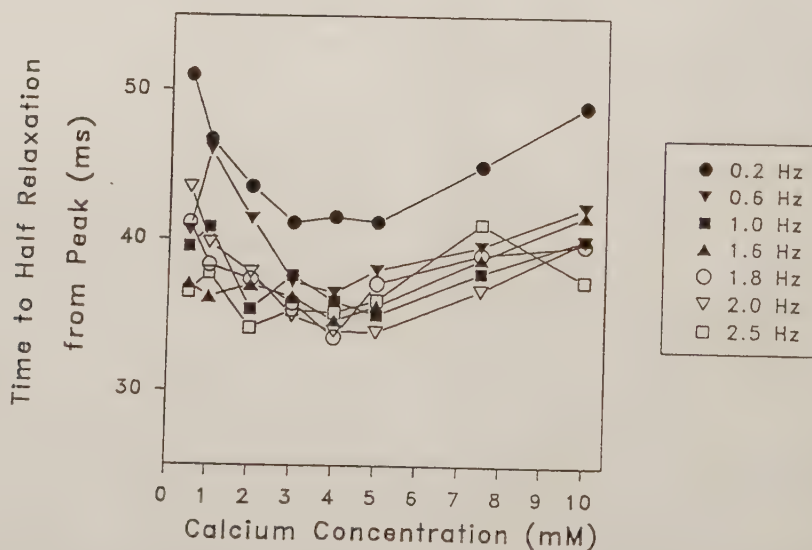


FIG. 5. Relaxation time (time from peak force to 50% peak force) as a function of extracellular calcium concentration and stimulation frequency (see legend) in atrial strips from skipjack tuna. Each point is the mean of six values, and the SE (not shown for purposes of clarity) averaged less than 6% (range 0.7–11.4%) of the mean.

20%) and hagfish (*Myxine glutinosa*, 40%), but less than that of little skate (*Raja erinacea*, 500%) and black dogfish (*Etmopterus spinax*, 580%).

The activation duration generally decreased with increasing calcium concentration over a range of 0.5–5.0 mM Ca_0^{2+} at all stimulation frequencies tested (Fig. 4). At concentrations

greater than 5.0 mM Ca_0^{2+} , no further calcium-dependent reductions in activation duration were observed. Activation duration was also affected by stimulation frequency, being reduced with increasing stimulation rate over a range of 0.2–1.0 Hz (Fig. 4). Above 1.0 Hz, no further effects of frequency were found.

Relaxation times (Fig. 5) were generally reduced with increasing Ca_0^{2+} over the range of 0.5–4.0 mM. Increasing Ca_0^{2+} above 4.0 mM resulted in an increase in relaxation time. Like activation, increasing stimulation frequency decreased the duration of relaxation events, but only at the lowest frequencies tested (0.2–0.6 Hz).

Adrenaline concentration–response curves (Fig. 6) and EC_{50} values were not significantly affected by rate ($p > 0.05$). Force development was increased by adrenaline concentrations over a range of 10^{-8} to 10^{-5} M, with an EC_{50} value of $4.90 \pm 0.57 \times 10^{-7}$ M. In most instances, concentrations above 10^{-5} M decreased force somewhat, likely as a result of desensitization processes. In some trials, a slight decline in force production from control was observed at adrenaline concentrations below 10^{-8} M. This could reflect incomplete washout of adrenaline from the tissue after previous trials. Activation and relaxation durations were not found to be significantly ($p > 0.05$) altered by either adrenaline application or stimulation frequency (data not shown). No significant changes in passive force were observed with adrenaline application at any concentration.

Discussion

The force–frequency relationship for skipjack tuna atrial strips was unlike that of mammalian atrial preparations (Gibbons 1986). With increasing stimulation frequency, peak active force increased to a maximum and then declined at higher rates. The majority of mammalian atria demonstrate a three-component response to increasing frequency: force initially declines at low stimulation rates, then increases, and finally decreases at high frequencies. The tuna atrial curve was thus biphasic rather than triphasic and resembles, in this regard, results for ventricular preparations of mammals (Woodworth 1902; Blinks and Koch-Weser 1961), amphibians (Bowditch 1871; Niedergerke 1956), and elasmobranchs (Driedzic and Gesser 1988). It must be noted, however, that it is possible that the slowest stimulation rate used in this study was too high to detect force reductions associated with even lower frequencies.

The magnitude of the increase in force with increasing stimulation frequency was relatively modest, with peak force levels increasing by only about 50% over initial values (at 0.2 Hz). This is much less than the two- to three-fold increase in force that is typically found in atrial strip preparations from a variety of mammals (Gibbons 1986). In ventricular strips from Atlantic cod, sea raven (Driedzic and Gesser 1988), and carp (Vornanen 1989) only a decrease in force was found with increasing stimulation rate. The reasons underlying the differences in the force–frequency relationship are not readily apparent, but likely reflect species differences in processes involved in calcium storage and release (Blinks and Koch-Weser 1961). In this regard, we revealed, through the use of ryanodine, one important difference between skipjack tuna and all other fish species examined thus far. It appears contraction in the skipjack tuna is dependent to a significant degree on intracellular stores.

In mammals most of the activator calcium is thought to be derived from SR stores, with calcium influx across the sarcolemma serving primarily as the trigger for SR calcium release (Fabiato 1983). Ryanodine is a natural plant alkaloid that, at micromolar concentrations, blocks SR calcium release (Sutko and Kenyon 1983). Tissue sensitivity to ryanodine is considered to reflect the dependence of contractility on release from intracellular stores. Ventricular tissue from frog (Nayler 1963;

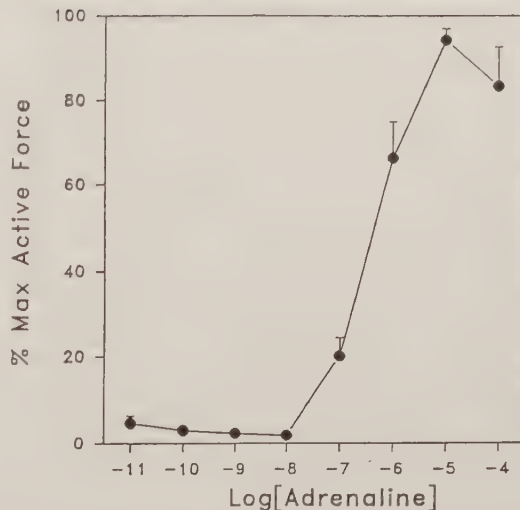


FIG. 6. Change in force development of skipjack tuna atrial strips as a function of adrenaline concentration. The concentration–response curve and estimated EC_{50} were not affected by stimulation frequency ($p < 0.05$). Adrenaline values are expressed as the log of the concentration. Force values are expressed as a percentage of maximal force and are given as means $\pm$ SE unless error bars are smaller than symbol radius. Stimulation frequency in this instance was 1.0 Hz. Mean EC_{50} was estimated to be 5.13×10^{-7} M at this rate. $N = 6$.

Bers 1985) and rabbit (Sutko and Willerson 1980) is relatively insensitive to ryanodine treatment whereas contractility in rat (Bers 1985; Stemmer and Akera 1986) and mouse (Stemmer and Akera 1986) is greatly depressed. Cod and sea raven cardiac muscle strips are insensitive to ryanodine (Driedzic and Gesser 1988) whereas rainbow trout ventricular strips show limited sensitivity to ryanodine, depending upon the protocol (Gesser and Hoglund 1988; Hove-Madsen and Gesser 1989) and incubation conditions used (El-Sayed and Gesser 1989). Ryanodine application to tuna atrial strips was found to depress active force generation by approximately 20–30%, the magnitude being dependent upon the stimulation frequency. Assuming that, as in mammals, mitochondria are normally unimportant in supplementing contractile calcium and that the binding characteristics of ryanodine are similar in fishes and mammals, the calcium responsible for activation of force in the tuna heart must be derived from at least two sources. While the bulk of activator calcium is derived from extracellular sources, a significant fraction is supplied by internal stores (i.e., the SR).

Direct activation of myofilaments via calcium influx has been suggested in lower vertebrates (Morad *et al.* 1983; Vornanen 1989; Tibbitts *et al.* 1990, 1991). It has been demonstrated in frog cardiac tissue by means of a variety of electrophysiological and pharmacological arguments that the magnitude of calcium influx across the sarcolemma is sufficient to directly activate the myofilaments (Morad *et al.* 1983; Morad and Cleeman 1987). Similar anatomical and biochemical features are apparent in fishes and frogs. In fishes (Santer 1985) and in frogs (Page and Niedergerke 1972), the SR is loosely organized and is sparse in comparison with that of mammals. Myocyte diameters in both frogs and fishes are typically much less than

10 μm (Page and Niedergerke 1972; Santer 1985). Lastly, under physiologically relevant conditions, ryanodine does not have a significant impact on force development in frog and all other fishes examined except the tuna. Thus, the tuna heart is like other fishes in that contraction is primarily dependent upon sarcolemmal influx rather than sarcoplasmic reticular release. However, unlike other fishes, a large contribution to the calcium pool responsible for contraction in the tuna heart is derived from the SR, as in many mammals.

Heart rates in most lower vertebrates do not exceed 120 bpm (Farrell 1991). While a number of components are likely involved in attainment and maintenance of high heart rates (nerve conduction velocities, densities and capacities of channels, exchangers and pumps, myosin isoforms, etc.), a contributing limitation may be the intracellular diffusion distance that calcium must cross to activate myofilaments. The diameter of cardiac myocytes of upper vertebrates generally exceeds 10 μm (Muir 1965; Sommer and Johnson 1979) and, given the heart rates found in most lower vertebrates, the implication is that it is too great to support high (>120 bpm) heart rates. This is circumvented in higher vertebrates by infoldings of the sarcolemma that invaginate the myocyte and form a junctional complex with the calcium-release sites of the terminal cisternae of the SR (McNutt 1975). Diffusional distances are secondarily reduced by utilizing the SR, which is in close proximity to the myofilaments, as an intracellular source of activator calcium. The transverse tubule system found in mammals is not found in any fishes, including the tuna (Santer 1985); however, myocyte diameters in a related species of tuna, *Thunnus alalunga*, have been reported as 2.5–6.0 μm (Breisch *et al.* 1983) and the small intracellular diffusional distance, in conjunction with a functional store of SR calcium, may permit the high heart rates found.

The Ca_0^{2+} -response trials demonstrated changes in active force generation to be greatest over Ca_0^{2+} concentration range of 1.0–5.0 mM (Fig. 3). Plasma calcium concentration values for tuna are within this range (4.2–7.6 mM; Sather and Rogers 1967; Bourke *et al.* 1987) and, assuming free calcium to account for ~60% of the total plasma calcium pool (Driedzic and Gesser 1985), agents that alter calcium influx (such as adrenaline) represent an attractive method of increasing force production. This was also reflected by changes in activation and relaxation durations.

Increases in Ca_0^{2+} concentration were found to decrease the amount of time required to reach peak force generation (Fig. 4). Activation duration is a consequence of calcium influx and delivery to the myofibrils. With increasing Ca_0^{2+} , the time taken to fully activate contractile proteins should decline to a level at which force development is limited by diffusional distances (both to the SR and myofilaments) and not by any further increases in Ca_0^{2+} . This limiting concentration appears to approximate 5.0 mM calcium in tuna atrial strips.

Relaxation duration is related to the ability of efflux mechanisms to remove cytosolic calcium and its association with contractile proteins. Relaxation rates declined with increasing Ca_0^{2+} over a range of 0.5–4.0 mM (Fig. 5) and increased at higher concentrations. The apparent confounding relationship of a decrease in duration time despite an assumed greater cytosolic calcium load cannot be readily explained but may result from a balance between the affinity of efflux mechanisms for calcium and the capacity of the SR and mitochondria to store calcium. Indeed, were transport and storage mechanisms to approach saturation, the relaxation duration should increase as

is found at Ca_0^{2+} levels in excess of 4.0 mM. This must be taken to be purely speculative at this juncture, as nothing is known about the action potential in tuna heart cells and the changes brought about by changes in Ca_0^{2+} .

Stimulation frequency also had an effect on activation and relaxation times, independent of Ca_0^{2+} levels. The mechanisms behind these events are beyond the scope of this paper but likely reflect alterations in both the quantity and rate of calcium flux to and from the myofilaments (Lewartowski and Pytkowski 1987). It is interesting to note, however, that the stimulation frequencies at which contractile cycle durations were minimized were ~1.0–1.6 Hz. This range of stimulation frequencies lies at or near the apex of the force–frequency relationship, and similar mechanisms may be responsible for both.

Lastly, the positive inotropism of cardiac muscle to adrenaline was examined through sequential addition to atrial strips. One of the actions of adrenaline is to increase the calcium influx through sarcolemma-bound L-type calcium channels (Reuter *et al.* 1986). Dose–response curves estimated an EC_{50} for adrenaline of 4.90×10^{-7} and demonstrated an operational range of 10^{-8} to 10^{-5} M. This is consistent with *in vivo* adrenaline levels in tuna (Watson 1990).

In summary, the tuna heart derives a large portion (~30% at resting stimulation frequencies) of activator calcium from intracellular stores, as shown in ryanodine trials, and resembles mammalian cardiac tissue in this regard more closely than other fishes. Perhaps not coincidentally, the heart rate of tuna is the highest of any lower vertebrate and approaches mammalian values. Unlike mammals, most of the contractile function appears to depend upon extracellular calcium supply rather than intracellular release, making modifications in calcium influx an attractive method of modifying force development in a tissue that is rather insensitive to rate changes in force production. This is supported by the high tissue sensitivity to changes in extracellular calcium at plasma calcium levels and to potential changes in intracellular calcium levels brought about by the action of adrenaline.

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Optimal Harvest Rates for Mixed Stocks of Natural and Hatchery Fish

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Optimal harvest rates were computed using dynamic programming for mixed-stock fisheries exploiting two stocks of either natural or hatchery origin. Natural stocks were described by a Ricker spawner–recruit relationship and hatchery stocks were described by a rectilinear spawner–recruit relationship. Harvest rates were optimized for both risk-neutral and risk-averse utility functions. For two natural stocks with low productivities, optimal harvest rates generally appeared to favor the stronger stock for a risk-neutral utility function and the weaker stock for a risk-averse utility function. For both utility functions, optimal harvest policy became less sensitive to relative stock strength as the productivity of the stocks increased. When at least one of the stocks was of hatchery origin, optimal harvest policy favored the weaker stock using either utility function.

En utilisant une programmation dynamique, l'auteur a calculé des taux d'exploitation optimum dans le cas de pêches axées sur deux stocks, soit d'origine sauvage ou d'élevage. Il a décrit les stocks d'origine sauvage à l'aide d'une relation géniteur–recrue de Ricker et les stocks d'élevage, d'une relation rectilinéaire géniteur–recrue. Il a ensuite optimisé les taux d'exploitation des fonctions d'utilité à risque neutre et à aversion pour le risque. Dans le cas de deux stocks naturels à faible taux de productivité, les taux d'exploitation optimum semblaient généralement favoriser le plus important stock pour ce qui est de la fonction d'utilité à risque neutre, et le stock le moins abondant pour ce qui est de la fonction d'utilité à aversion pour le risque. Dans le cas des deux fonctions d'utilité, une politique d'exploitation optimum a moins réagi à l'abondance relative d'un stock lorsque la productivité des stocks augmentait. Lorsque au moins un des stocks était issu de l'élevage, une politique d'exploitation optimum favorisait le stock moins abondant pour ce qui est des deux types de fonctions d'utilité.

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Mixed-stock fisheries present some complex and persistent problems in the management of renewable resources. Problems associated with identification of spawner–recruit relationships (Ricker 1973; Hilborn 1985a), loss of stock diversity (Ricker 1958; Paulik et al. 1967), and optimal harvest from mixed-stock fisheries (Ricker 1958; Paulik et al. 1967; Hilborn 1976, 1985b; Collie et al. 1990) have all been investigated using Pacific salmon as examples. Pacific salmon stocks are particularly suited for investigating mixed-stock problems. Because of their fidelity to natal streams, individual salmon stocks can be clearly identified on the spawning grounds, and it is possible to monitor individual stocks over time. Virtually all salmon fisheries harvest a mixture of stocks that can differ widely in size, productivity, and variability. Natural salmon production is also supplemented by production from hatcheries that have been constructed to mitigate the impacts of water development projects and to enhance fisheries. Hatcheries are typically more productive than natural stocks in the sense that they produce more recruits per spawner than do naturally spawning stocks. The proliferation of hatcheries has prompted concerns that fisheries supported by hatchery stocks may severely deplete less productive natural stocks (Wright 1981).

The particular problem addressed here is that of optimal harvest of mixed stocks by a common fishery. Ricker (1958) presented a graphical solution to this problem and showed that maximum equilibrium yield for mixed-stock fisheries could, in some cases, be obtained at harvest levels that would drive some

component stocks to extinction. Paulik et al. (1967) derived a general solution demonstrating that maximum sustainable yields from mixed-stock fisheries may entail elimination of less productive stocks, and declines in the spatial heterogeneity of Pacific salmon stocks have been observed coincident with increasing fishing mortality rates (Walters and Cahoon 1985).

Hilborn (1976), using dynamic programming, investigated optimal harvesting of two stocks by a common fishery. This technique allows for inclusion of uncertainty about future production and relaxation of the assumption of equilibrium conditions. Hilborn (1976) solved for optimal harvest rates for specific combinations of stock abundances, demonstrated that optimal harvest rates depend on the relative abundance of the component stocks, and concluded that, in general, mixed-stock fisheries should be harvested more heavily when the ratio of stocks differs from 1:1. Optimal harvest policies determined by dynamic programming assume that managers have the ability to forecast the abundance of individual stocks that contribute to a mixed-stock fishery. Hilborn (1985b) later pointed out that the requirement of individual forecasts for the component stocks was unrealistic and sought optimal management strategies from a class of strategies that does not require forecasting of individual component stocks.

In this paper, I use dynamic programming to evaluate harvest strategies that optimize risk-neutral (Hilborn 1976; Mendelssohn 1982; Deriso 1985) and risk-averse (Mendelssohn 1982; Deriso 1985; Walters and Ludwig 1987; Parma 1990) utility functions for a single fishery harvesting two stocks.

The spawner–recruit relationships (SRRs) used to model stock dynamics are chosen to represent naturally produced fish and hatchery-produced fish. I also reexamine optimal harvest policies for a fishery harvesting two natural stocks using a finer grid for stock sizes and a broader range of parameter values than were used by Hilborn (1976). I show that the functional forms of the SRRs and the utility function can profoundly affect optimal harvest strategies. Although I examine only a few specific cases for two-stock fisheries, the results suggest some general conclusions that may be applicable to cases where individual stock forecasts are not possible and to cases involving more than two stocks.

Methods

Following Hilborn (1976), I used a Ricker SSR to describe recruitment to a natural population. The particular form used was

$$(1) R_{t+1} = S_t \exp[\alpha[1 - (S_t/\beta)] + \epsilon_t]$$

where R_{t+1} is the number of recruits resulting from S_t spawners, α is a productivity parameter (specifically, the natural log of the number of recruits produced by each spawner in the absence of density-dependent effects), β is the equilibrium stock size (i.e. the level of spawning escapement where each spawner exactly replaces itself in the absence of fishing mortality), and ϵ_t are independently distributed normal random variables with zero mean and variance σ^2 . Hatchery stocks were assumed to have a rectilinear SRR of the form

$$(2) R_{t+1} = \min(\alpha S_t, \beta) \exp(\epsilon_t).$$

This functional form presumes that recruitment of hatchery fish is, on average, proportional to the number of fish spawned at the hatchery, with no density dependence when the abundance of spawners is less than the hatchery capacity. If the number of spawners exceeds the hatchery capacity, the excess spawners have no effect on recruitment.

Omitting age structure and natural mortality, recruitment equals preharvest abundance, simplifying both the population model and the optimization problem. The description of population dynamics is completed by

$$(3) S_t = R_t - C_t$$

where C_t is catch from generation t in numbers of fish and harvest rate is defined as

$$(4) h_t = C_t / R_t.$$

I computed approximately optimal harvest policies using dynamic programming following the procedure outlined in Hilborn (1976), but using a finer discretization. Where Hilborn (1976) used 20 abundance levels, 18 harvest rates, and 10 stochastic outcomes, I used 80 abundance levels, 40 harvest rates, and 20 stochastic outcomes with $\sigma = 0.5$. This finer discretization increases the resolution of the approximate solutions and reveals details that are not readily apparent on the coarser grid.

Hilborn (1976) observed that for two stocks governed by equation (1), there are five nonredundant possibilities for the stock–recruitment dynamics: (1) $\alpha_1 = \alpha_2$, $\beta_1 = \beta_2$, (2) $\alpha_1 > \alpha_2$, $\beta_1 = \beta_2$, (3) $\alpha_1 = \alpha_2$, $\beta_1 > \beta_2$, (4) $\alpha_1 > \alpha_2$, $\beta_1 > \beta_2$, and (5) $\alpha_1 > \alpha_2$, $\beta_1 < \beta_2$. Other possible relation-

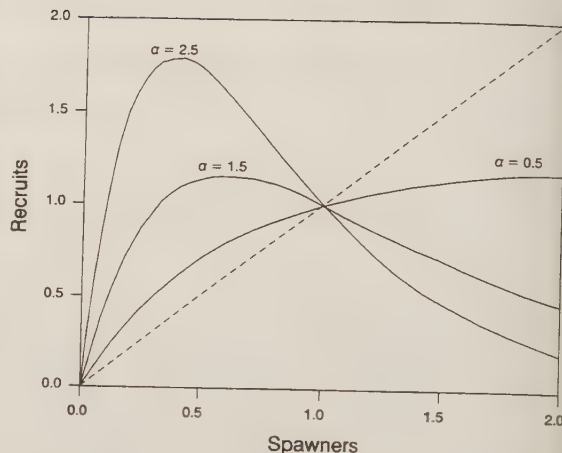


FIG. 1. Spawner–recruit curves used for the “natural” stocks in the dynamic programming estimation of optimal harvest rates for low-productivity stocks ($\alpha = 0.5$), moderate-productivity stocks ($\alpha = 1.5$), and high-productivity stocks ($\alpha = 2.5$). Unexploited equilibrium stock size (β) is equal to 1.0.

ships involve simply interchanging stock 1 and stock 2. However, in addition to depending on the relative magnitudes of the stock productivities (i.e. the ratio of α_1 to α_2), optimal harvest strategies also depend on the absolute magnitude of the stock productivities with every unique combination of productivities producing a unique solution. In contrast, the equilibrium stock levels serve merely to scale the spawner–recruit curves, and a constant ratio of β_1 to β_2 will always produce the same solution relative to equilibrium stock sizes regardless of the absolute magnitude of the equilibrium stock sizes. Because it is impossible to examine all potential combinations of α and β , I considered only a limited number of cases. I examined optimal harvest rates for stocks of low ($\alpha = 0.5$), moderate ($\alpha = 1.5$), and high ($\alpha = 2.5$) productivities (Fig. 1) and with either identical β s or β s that differed by a factor of 2. Solutions were obtained for both risk-neutral and risk-averse objective functions by maximizing either the sum of expected catches over the planning horizon or the sum of the natural logarithms of expected catches over the planning horizon. Both of these utility functions are maximized in the last time period by harvesting the entire stock. As we work backward in time, the expected contribution of future catches to the objective function increases and lower harvest rates maximize the objective functions. Working backward from the last time period, optimal harvest strategies usually stabilize within 10 yr. In all cases presented here, harvest rates were optimized by calculating backward over a 20-yr planning horizon.

Results

Two Natural Stocks

For each possible combination of stock sizes, the dynamic programming algorithm computes the harvest rate that optimizes the objective function by maximizing the utility of the catch obtained in the present time period and the expectation of future catches from the spawning escapement. For a single

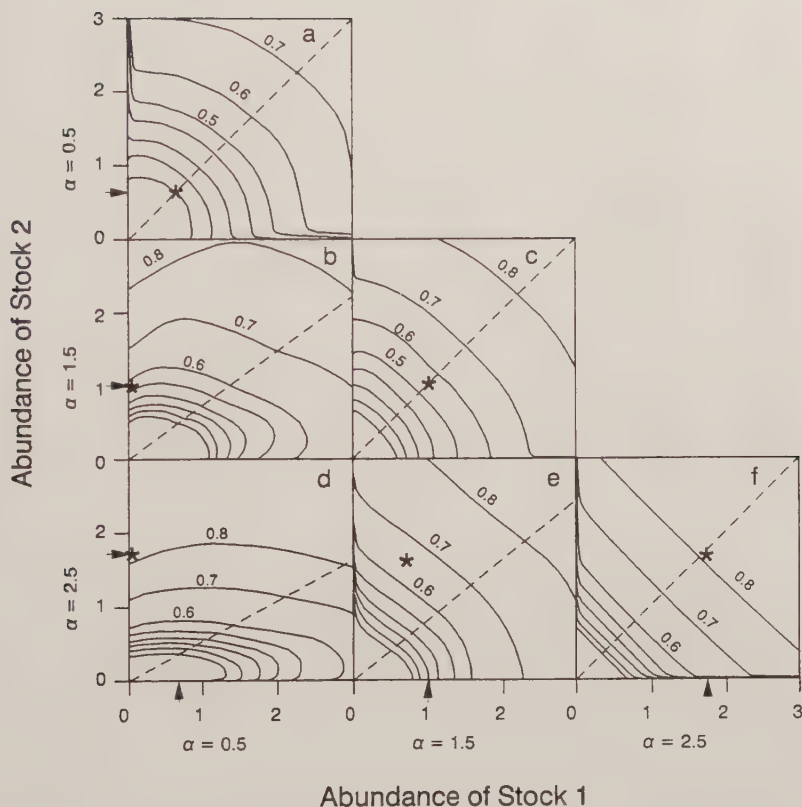


FIG. 2. Optimal risk-neutral harvest rate contours for stocks with identical unexploited stock size ($\beta = 1.0$). Individual stock MSY equilibria are indicated by arrows on the figure axes, and the joint MSY equilibria are indicated by asterisks. The broken line indicates isoharvest proportions where identical harvest rates are optimal for both individual stocks.

stock governed by the Ricker SRR the harvest policy that optimizes the linear (risk-neutral) utility function is to harvest that portion of the recruitment (abundance) that is in excess of some optimal spawning escapement. If abundance falls below this optimal escapement, then no harvest is taken and the stock is allowed to rebuild (Walters 1975; Parma 1990). Associated with each nonzero harvest rate is a single abundance level for which that harvest rate is optimal. In a two-stock fishery, the combinations of component stock abundances that share the same individual optimal harvest rates describe a path through the stock abundance plane. Along this trajectory, which I will call the "isoharvest" line, the optimal harvest rate for the mixed-stock fishery is also optimal for each component stock individually (Fig. 2). For combinations of stock abundances that lie above the isoharvest line, the harvest rates that would be optimal for the stock plotted on the ordinate (stock 2) are higher than the optimal harvest rates for the stock on the abscissa (stock 1). Thus, above the isoharvest line, stock 2 is, in a sense, the stronger stock and stock 1 the weaker stock. For any stock abundance combination that does not lie on this isoharvest line, the optimal harvest rate in the mixed-stock fishery will be intermediate between the harvest rates that are optimal for the two component stocks at their respective abundances.

When the two component stocks are governed by identical SRRs the isoharvest line is a straight line with slope 1.0 (Fig. 2a, 2c, and 2f). Stock combinations producing constant levels of total abundance describe straight lines in the stock abundance plane with slopes of -1.0 . If optimal harvest rates depend only on the overall abundance, and not on the stock composition, optimal harvest rate contours will coincide with these constant levels of total abundance. If contours of optimal harvest rates deviate from these straight lines with slope -1.0 , the optimal harvest policy is stock dependent.

The dependence of optimal harvest policy on stock productivities is readily apparent (Fig. 2). Hilborn (1976) reported that the optimal harvest policy for two identical stocks was a constant escapement policy which would be represented by straight contours with a slope of -1 . This is approximately true only when the stocks have high productivity (Fig. 2f). For low-productivity stocks (Fig. 2a), and to a lesser extent moderate-productivity stocks (Fig. 2c), the optimal harvest rate contours are concave. This means that for identical stocks with low productivities or moderate productivities, if the stock composition differs from the isoharvest ratio of 1:1, the optimal harvest rate is higher than it would be for the same total abundance partitioned equally among the two component

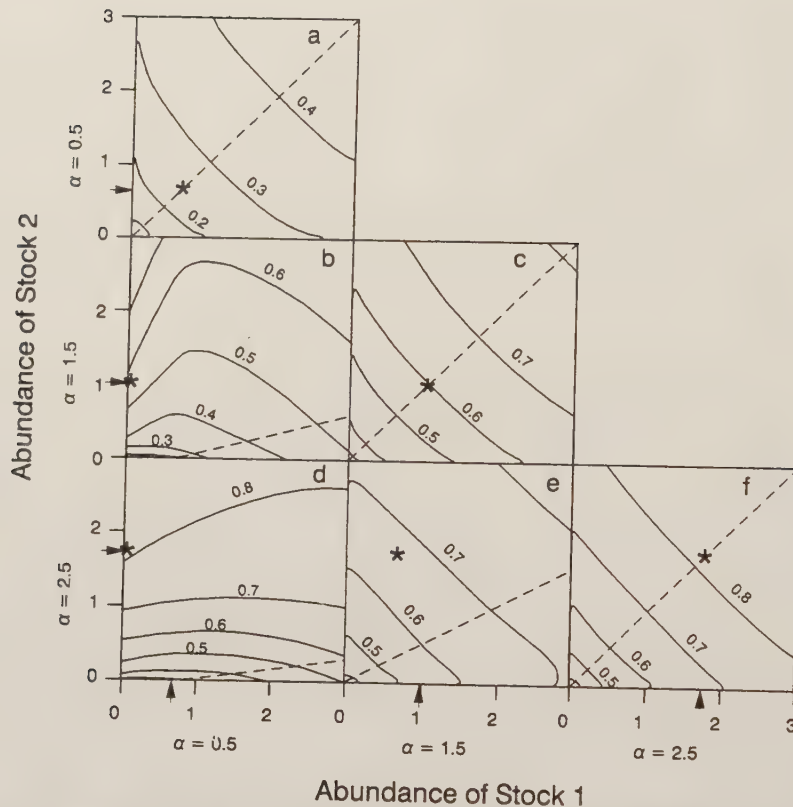


FIG. 3. Optimal risk-averse harvest rate contours for stocks with identical unexploited stock size ($B = 1.0$). Individual stock MSY equilibria are indicated by arrows on the figure axes, and the joint MSY equilibria are indicated by asterisks. The broken line indicates isoharvest proportions where identical harvest rates are optimal for both individual stocks.

stocks. For stocks with high productivities the optimal harvest rate contours are slightly convex, indicating that optimal harvest rates are slightly lower if abundance is not partitioned equally between the two component stocks, but the convexity is so slight that the optimal harvest policy could be considered stock indifferent for most reasonable abundance combinations.

While optimal harvest rates for all stock combinations are of interest, some stock combinations are far more likely to occur than others. Solutions presented here assume that future harvest rates will also be optimized, and continual management for optimal yields will tend to hold the stocks near the equilibrium levels that would support maximum sustainable yields in the absence of random variability (MSY equilibrium). If the low-productivity stock is harvested jointly with either the moderate- or high-productivity stocks, the low-productivity stock becomes extinct at MSY equilibrium (Fig. 2b and 2d). When MSY equilibrium supports only one stock, optimal harvest rates are understandably more sensitive to changes in the abundance of the stock that will remain at equilibrium than they are to changes in the stock destined for extinction. For the combination of moderate- and high-productivity stocks (Fig. 2e), MSY equilibrium results from a mixed-stock fishery and the optimal policy is nearly stock indifferent in the vicinity of this equilibrium. However, optimal harvest policy is more sensitive

to the less productive stock if it is either at extremely low levels or at high levels relative to the more productive stock, reducing harvest rates if the less productive stock is in danger of extinction and increasing harvest rates if it becomes superabundant.

Optimal risk-averse harvest policy is less dependent on overall abundance, with higher harvest rates at low stock levels and lower harvest rates at high stock levels, than risk-neutral management (Fig. 3). This is consistent with the tendency for optimal risk-averse policies to approach constant harvest rates, producing less variability in catches. The decrease in variability of harvest rates produces a greater disparity in the isoharvest abundance ratios for stocks that differ in productivity (Fig. 3b, 3d, and 3e). Like optimal risk-neutral harvest policies, optimal risk-averse policies are less sensitive to stocks destined for extinction at the MSY equilibrium (Fig. 3b and 3d). In the remaining cases, where the MSY is obtained from a mixed-stock fishery, the deviations in optimal harvest rates associated with variation in stock composition appear to be the opposite of deviations in optimal risk-neutral harvest policy. For low-productivity stocks, optimal policy decreases harvest rates when the composition of stocks is inequitable, and the stock dependency of optimal harvest policy decreases as stock productivity increases.

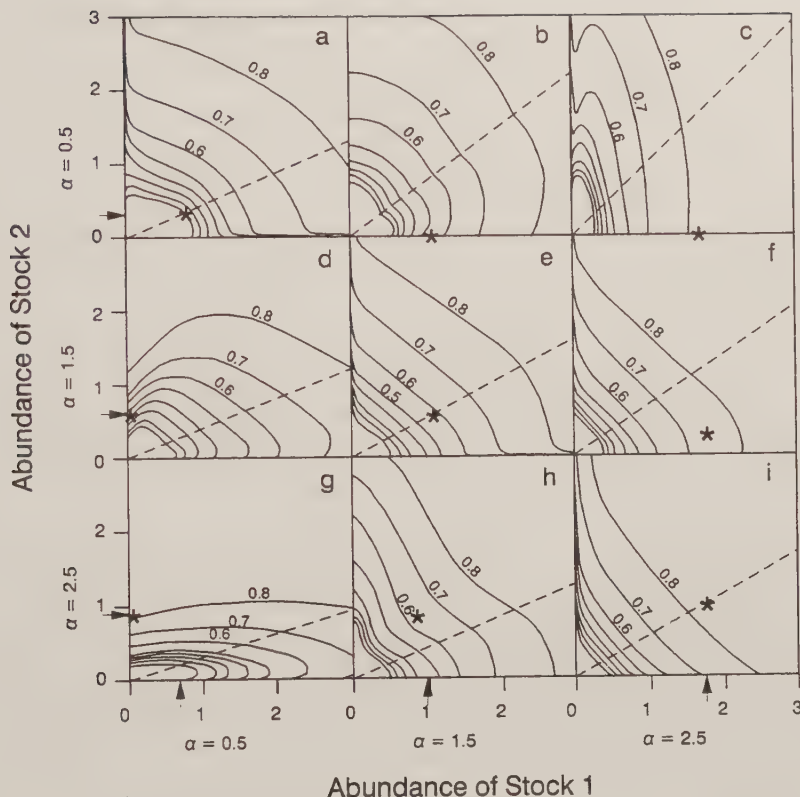


FIG. 4. Optimal risk-neutral harvest rate contours for stocks with different unexploited stock equilibria ($\beta_1 = 1.0$, $\beta_2 = 0.5$). Individual stock MSY equilibria are indicated by arrows on the figure axes, and the joint MSY equilibria are indicated by asterisks. The broken line indicates isoharvest proportions where identical harvest rates are optimal for both individual stocks.

For two natural stocks with different β s, optimal risk-neutral and risk-averse harvest policies are qualitatively similar to corresponding cases with identical β s (Fig. 4 and 5). In all cases, optimal harvest rates are less sensitive to stocks that will be extinct at the MSY equilibrium than to the stocks that will survive. Again, optimal risk-averse harvest policy is less sensitive to the relative abundance of the two component stocks at a given level of overall abundance than is risk-neutral management. Of particular interest is the case of a moderate-productivity stock with large β and a high-productivity stock with small β under risk-neutral management (Fig. 4h). With this combination of stocks, the expected contributions from the two component stocks to the combined yield are very similar. In the vicinity of the MSY equilibrium, there is a ridge in the optimal harvest rate contours. This depicts an optimal harvest strategy that decreases harvest rates when the ratio of stock abundances differs from the equilibrium ratio at MSY.

Hatchery and Natural Stocks

The optimal risk-neutral harvest strategies for mixed fisheries of hatchery and natural stocks differ dramatically from those involving two natural stocks (Fig. 6). An abrupt ridge occurs in the optimal harvest rate contours coincident with the

isoharvest line, and optimal harvest rates decrease as the ratio of stocks departs from the isoharvest ratio. The MSY equilibrium entails far greater relative abundance of the hatchery stock than the isoharvest ratio. In all cases the MSY equilibrium occurs with both stocks present and the hatchery stock at its individual MSY abundance level, but bear in mind that the rectilinear SRR used for the hatchery stock ensures that the expected abundance of the hatchery stock is constant unless harvest rates are greater than the productivity of the hatchery stock. The MSY equilibrium for the natural stock is noticeably less than its individual MSY level only in the case where the unfished equilibrium for the hatchery stock is larger than that of the natural stock. In the region of the MSY equilibrium the optimal harvest rates are much more sensitive to changes in the natural stock than to changes in the hatchery stock.

Under risk-averse management, this prominent ridge in the optimal harvest rate contours is even more pronounced (Fig. 7). Again, optimal risk-averse harvest rates are less sensitive to changes in total abundance than are optimal risk-neutral harvest rates. However, unlike cases involving two natural stocks, optimal harvest rates are more sensitive to changes in the stock composition than are harvest rates under risk-neutral management. In the region of the MSY equilibrium, which is now even

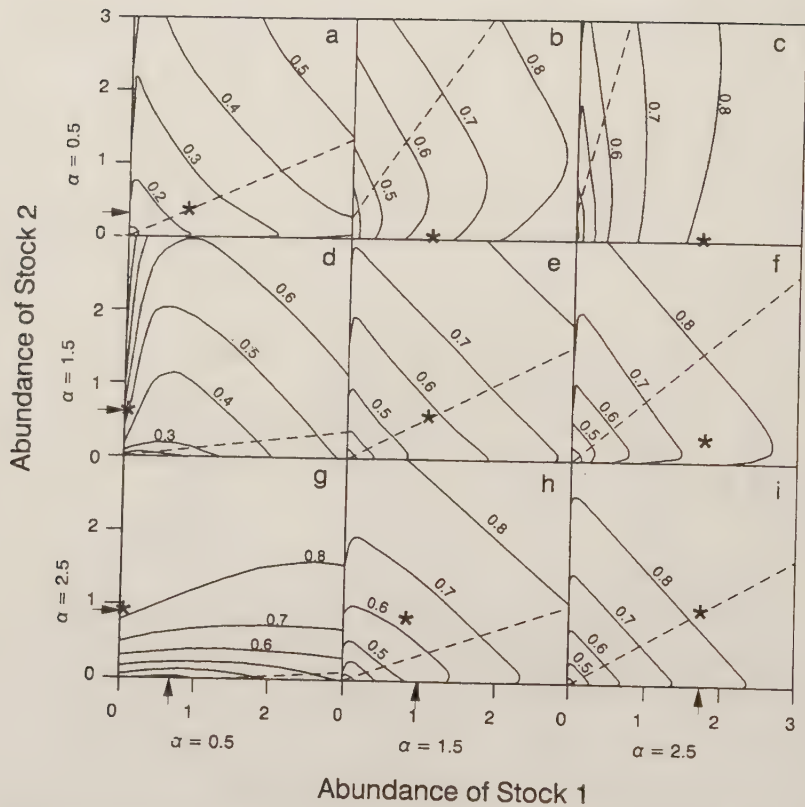


FIG. 5. Optimal risk-averse harvest rate contours for stocks with different unexploited stock equilibria ($\beta_1 = 1.0$, $\beta_2 = 0.5$). Individual stock MSY equilibria are indicated by asterisks on the figure axes, and the joint MSY equilibria are indicated by arrows. The broken line indicates isoharvest proportions where identical harvest rates are optimal for both individual stocks.

further from the isoharvest line, optimal harvest rate contours are vertical, indicating that optimal harvest policy is independent of changes in the hatchery stock.

The presence of the sharp ridge in the optimal harvest rate contours for mixed-stock fisheries results from the rectilinear SRR used for the hatchery stock. Above the isoharvest line the combinations of hatchery stock abundance and harvest rates that are optimal for the natural stock ensure that hatchery spawners will exceed hatchery capacity. Changes in the harvest of hatchery fish have no effect on future stock dynamics, only on harvest at the present time. At the same time, changes in the harvest of natural fish affect both the current harvest and future harvests. Consequently, optimal harvest rates are more sensitive to abundance of the natural stock than of the hatchery stock. Below the isoharvest line the hatchery stock is at sufficiently low abundance that harvest rates that are optimal for the natural stock will fail to provide enough hatchery spawners to fully utilize hatchery capacity. At this point, optimal harvest rates are driven by full utilization of hatchery capacity unless the disparity in stock sizes is so great that the cumulative loss from underharvesting the natural stock would exceed the loss from a one-time failure to fully utilize hatchery capacity. If we remove the abrupt transition in the hatchery SRR, by substituting a Beverton-Holt SRR for the rectilinear SRR, the ridge in the optimal harvest rate contours nearly disappears, as does much of the dependence on hatchery stocks (Fig. 8).

tuting a Beverton-Holt SRR for the rectilinear SRR, the ridge in the optimal harvest rate contours nearly disappears, as does much of the dependence on hatchery stocks (Fig. 8).

Discussion

Equilibrium analyses can place an upper limit on the average yield that can be expected from a mixed-stock fishery, and the component stocks that will still be around at equilibrium to contribute to this yield, but real fisheries are perpetually in a state of disequilibrium. Dynamic programming can approximate optimal harvest policies that embrace disequilibrium and uncertainty for specified SRRs, but the computational burden limits the size and complexity of problems that can be addressed. While the optimal harvest rates in any particular case depend on the SRRs chosen to describe stock dynamics and the specific parameter values used, a few general axioms can be inferred from the simulations presented here.

(1) For unproductive natural stocks, optimal risk-neutral harvest rates are more sensitive to changes in the stronger stock and optimal risk-averse harvest rates are more heavily influenced by the weaker stock.

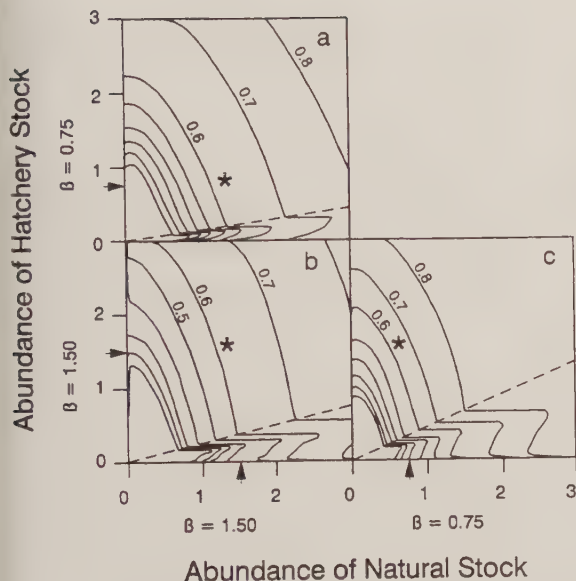


FIG. 6. Optimal risk-neutral harvest rate contours for stocks with different production functions. The natural stock is governed by a Ricker SRR with moderate productivity ($\alpha = 1.5$), and the hatchery stock is governed by a high-productivity ($\alpha = 2.5$) rectilinear SRR. Individual stock MSY equilibria are indicated by arrows on the figure axes, and the joint MSY equilibria are indicated by asterisks. Isoharvest proportions occur along the broken lines.

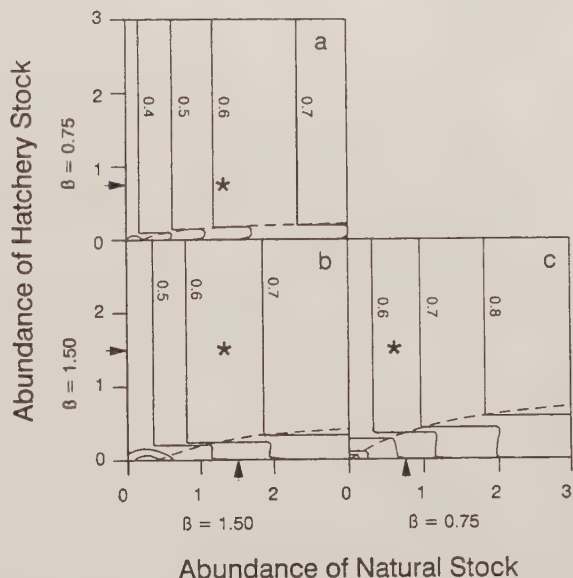


FIG. 7. Optimal risk-averse harvest rate contours for stocks with different production functions. The natural stock is governed by a Ricker SRR with moderate productivity ($\alpha = 1.5$), and the hatchery stock is governed by a high-productivity ($\alpha = 2.5$) rectilinear SRR. Individual stock MSY equilibria are indicated by arrows on the figure axes, and the joint MSY equilibria are indicated by asterisks. Isoharvest proportions occur along the broken lines.

(2) Over a fairly broad range of stock productivities, the stock dependence of both risk-neutral and risk-averse optimal harvest rates decreases as stock productivity increases.

(3) In hatchery-enhanced fisheries, jointly optimal harvest rates are more heavily influenced by the weaker stock over a fairly broad range of stock abundance combinations. The higher productivity of hatchery stocks ensures that the natural stock will nearly always be weaker than the hatchery stock.

While it is unlikely that stock forecasting and harvest regulation in mixed-stock fisheries will ever have the accuracy necessary to attempt to regulate harvest based on the relative abundance of individual stocks on a season by season basis, these axioms do have applicability to long-term management strategies. While short-term forecasting may be unreliable, it is widely accepted that a number of natural salmon stocks in California, Oregon, and Washington are chronically depressed (Nehlsen et al. 1991). Overharvest has been identified as a factor contributing to the decline or hampering the recovery of most of these stocks. Preservation of genetic diversity and variability are often invoked as reasons for restoring depressed natural stocks, but the results presented here indicate that by criteria based on yield alone, these stocks should be restored. Harvest rates that optimize the expected yield from mixed-stock fisheries for hatchery and natural fish should routinely produce healthy runs of natural spawners and substantial surpluses of hatchery spawners. This implies that yields from fisheries that cannot discriminate between natural and hatchery stocks could be increased by reducing the harvest rates to rebuild depressed natural stocks.

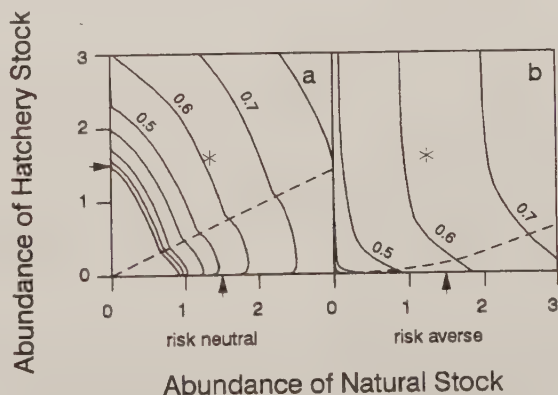


FIG. 8. Optimal harvest rate contours for a mixture of hatchery and natural stocks with hatchery stocks governed by a Beverton-Holt SRR. (a) Risk-neutral utility function, analogous to Fig. 6b; (b) risk-averse utility function, analogous to Fig. 7b.

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Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction

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Synopsis

The age, growth, and sexual maturation of the leopard shark, *Triakis semifasciata*, from central California were studied. Growth band counts in vertebral centra of 162 leopard sharks produced von Bertalanffy growth curves with L_{∞} , K , and t_0 parameters of 1536 mm, 0.082, and -2.31 , respectively, for both sexes combined. The L_{∞} value for females (1602 mm TL) was slightly but insignificantly higher than for males (1499 mm TL), but the K and t_0 values were almost identical. Seasonal changes in size modes of young-of-the-year leopard sharks, centrum edge characteristics, and growth and tetracycline mark-recapture from the field were used to validate annual deposition of vertebral centrum band pairs. Sexual maturity was evaluated by the gonads and presence of sperm and eggs; males mature at 7 yr and at about 63% of asymptotic length, and females mature at 10 yr, and at about 72% of asymptotic length. This slow growth, late maturity, and relatively low fecundity may increase their susceptibility to over-exploitation.

Introduction

Elasmobranchs have become important fishery resources worldwide, yet many aspects of their ecology suggest that they may be susceptible to over-exploitation (Holden 1974, 1977). For most elasmobranchs, including those commercially fished, very little essential information on their life histories is available (Compagno 1984). In general, those studied exhibit relatively slow growth rates, late age at sexual maturity, and low fecundity (Holden 1973, 1974, 1977, Holden & Vince 1973, Ketchen 1975, Jones & Geen 1977a).

Establishing the temporal periodicity of growth

zone deposition in calcified body parts is essential to the complete understanding of fish growth (Beamish & McFarlane 1983, Cailliet et al. 1986, Cailliet & Radtke 1987). Various authors have postulated that these growth zones are deposited annually, but few critical tests of this hypothesis have been accomplished, especially for elasmobranchs (Brown & Gruber 1986, Smith 1984, Beamish & McFarlane 1985, McFarlane & Beamish 1987). Inaccurate estimates of ages result in very serious errors in the management and understanding of fish populations (Beamish & McFarlane 1983).

The leopard shark, *Triakis semifasciata*, is one of the commercially and recreationally important

shark species from California. It is distributed commonly in bays and nearshore water from Mazatlan, Mexico to Oregon, including the Gulf of California (Miller & Lea 1972, Castro 1983, Eschmeyer et al. 1984, Ebert 1986). Individuals obtain a maximum size of 1981 mm total length (Miller & Lea 1972). This shark is primarily a benthic feeder (Ackerman 1971, Russo 1975), and like many shark species, its diet varies with size and season (Compagno 1984).

Little is known about age determination or growth of the leopard shark. Determination of age of elasmobranchs is hampered by the lack of calcareous otoliths and cycloid or ctenoid scales. Several alternate methods of age determination have been developed for elasmobranchs (reviewed by Cailliet et al. 1983a, 1986). The most promising method is analysis of the growth bands deposited in calcified structures such as dorsal spines and vertebral centra. This approach, with a resin-embedding and sectioning process, was used by Smith (1984) to verify growth bands in tetracycline-labelled vertebrae. Prior to this, the only age determination technique applied to the leopard shark to date was size frequency analysis (Ackerman 1971).

Part of our study was initiated in 1979 at Moss Landing Marine Laboratories (MLML), California, to develop age determination techniques for use in producing a reliable growth curve, and to describe the size- and age-specific reproductive capabilities of the leopard shark in Elkhorn Slough, California. In the same year, a tagging study was initiated in San Francisco Bay, California by the National Marine Fisheries Service (NMFS), to determine if vertebral growth zones in leopard sharks formed annually. Using the first 12 oxytetracycline (OTC) marked and recaptured fish from the first three years of the NMFS study, the annual deposition of the growth zones was confirmed (Smith 1984). Also, other aspects of the population dynamics and fishery biology from this tagging study have been evaluated (Smith & Abramson 1990). Subsequent information from recaptured sharks from the NMFS study are updated herein, and combines with the results of the MLML study to produce more complete information on the growth and reproduction of this species.

Materials and methods

Leopard sharks were collected between March 1979 and June 1981 from Monterey and San Francisco Bays, California. Otter trawl and gill net samples in Monterey Bay, and hook and line catches at several angling contests (e.g. Herald et al. 1969) and power plant entrainment in Elkhorn Slough provided most (65%) of the specimens. Additional sharks were obtained from the San Francisco Bay NMFS tag-recapture study (Smith 1984, Smith & Abramson 1990).

Total length (TL) precaudal length (PCL), and girth to the nearest mm, and weight, to the nearest g, were recorded from each specimen. A section of 12 vertebrae was typically removed from below the origin of the first dorsal fin and frozen. For many specimens, clasper length (CL) was measured to the nearest mm and the reproductive tract was examined. Stage of development and the external outline of the Wolffian ducts (vas deferens) were recorded to assess reproductive condition in males (Pratt 1979). Sperm smears were examined microscopically to verify the presence of mature sperm. For females, the number and size of eggs in the ovaries were recorded, and newly fertilized eggs or embryos were counted, measured and sexed. Oviduct dimensions and degree of vascularization were also recorded. Females suspected of aborting young had oviduct vascularization and dimensions corresponding to observations for pregnant females.

To make the calcium-rich rings on the vertebral centra more visible, we first used a modified silver nitrate staining technique (Stevens 1975, Cailliet et al. 1983a), then used resin-embedding and sectioning techniques (Humason 1972, Smith 1984). A substitution reaction of silver for a calcium salt (usually a carbonate, phosphate or chloride) provided distinct silver-impregnated bands which became markedly dark after illumination under ultraviolet light.

To expose anterior and posterior centrum surfaces for staining, and to make the dimensions of each centrum uniform, the neural and haemal arches were cut away and the notochord remnants and

connective tissue were removed from each vertebra. For this procedure, the centra were immersed in bleach for 10–75 min, depending upon centrum size. The centra were rinsed thoroughly in distilled water and then soaked in concentrated formic acid for four min. Rinsed centra then were placed in 1% silver nitrate and exposed to ultraviolet light from 3–15 min until bands became discernible. Bound silver was fixed following a brief immersion in 5% sodium thiosulfate and non-specific background color was removed by a water rinse. Tetracycline-marked centra from the tag-recapture study were never stained, because the process involves decalcification and would have removed the fluorescent mark.

The staining technique resulted in highly visible bands near the center of the centrum surface, but the closely spaced bands near the centrum margin of larger sharks were not easily seen (Fig. 1). Also, larger centra required longer exposure to silver nitrate stain, which increased the resolution of central growth zones, but decreased the resolution of the peripheral bands. Therefore, all vertebrae were embedded in clear polyester casting resin and sectioned longitudinally at their widest diameters (Smith 1984). Sections (0.5 mm thick) were mounted on microscope slides with clear enamel and examined under a dissecting microscope at $25\times$ magnification with transmitted lighting.

Centrum diameter (CD) was plotted against TL of the shark. A least-squares linear regression analysis was used to test the hypothesis that CD increased with body size (TL). This is a requirement if centrum growth is to represent the growth of the shark.

The concentric bands differed from those described by Cailliet et al. (1983a) in that there were no fine rings within them. Two kinds of bands occurred: those which appeared transparent with transmitted light (poorly calcified), and those which were silver-nitrate stained and appeared black (highly calcified). The latter bands were initially assumed to be more heavily mineralized and to represent summer growth on the centrum (Jones & Geen 1977b). In the sections, only opaque bands that appeared in the corpus calcareum (see Brown

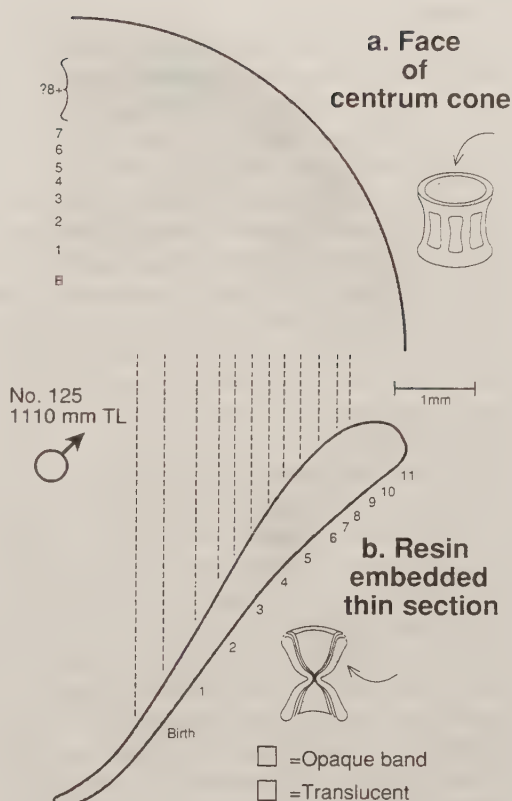


Fig. 1. Diagram comparing surface and thin-section band counts from the vertebral centrum of a male leopard shark (1110 mm TL): a – the anterior surface of the whole centrum stained with silver nitrate, showing 8 band pairs; b – an antero-dorsal thin section of the same centrum, showing 11 distinct bands.

& Gruber 1986) were counted (Fig. 1). Therefore, band counts refer to a complete pair of translucent and opaque bands.

Several centra from each specimen were processed to make sure that clearly stained specimens were available for study. To ensure precise, non-biased results, vertebral band counts were made without knowing specimen size, sex, or time of year collected. A consensus was reached among the two or three estimates of zone counts between readings.

Centra from 32 randomly chosen specimens were aged independently by two readers. Three

indices of band count precision were calculated: (1) average percent error (APE), measures the average deviation of each reading from the means of all readings of each section (Beamish & Fournier 1981); (2) percent error (D; Chang 1982), is calculated by dividing the coefficient of variation (V) of readings by the square root of the number of times each fish is aged (R), then multiplying this figure by 100. Chang (1982) suggested that D was a better estimator of precision because it is unbiased and consistent over all samples; and (3) the percent of the readings that agreed by $\pm 1, 2, 3$, etc. bands among all counts for the particular sample in question, also presented as a histogram of the percent agreement.

The von Bertalanffy growth function (VBGF; Bertalanffy 1938) was fitted to all the size and age data using FISHPARM (Prager et al. 1987). This program implements Marquardt's (1963) algorithm for least-square estimation of non-linear parameters. Standard errors and 95% confidence intervals were calculated for each of the three VBGF parameters (L_{∞} , K , and t_0). The VBGFs were calculated for both sexes combined and for each sex separately. Von Bertalanffy growth curves were plotted only for combined sexes. To substantiate the temporal periodicity of growth band deposition in vertebral centra, corroborative evidence was obtained from three sources. First, changes in size modes of young-of-the-year (YOY) leopard sharks were compared to the growth curve predicted from the VBGF from all aged specimens. YOY were collected in the spring and summer of 1979 through 1981 by otter trawl in the tidal creeks of Elkhorn Slough (Barry 1983). The first newborn (approximately 250 mm TL, with a slight umbilical scar remaining) leopard sharks to be caught in these collections indicated that birth occurred in May and June of each year, an observation previously made by Ackerman (1971). Starting in June, size modes were identified as means of individual TLs, and could be followed easily from month to month. Mean lengths and standard deviations were plotted on the growth curves from all aged specimens. The position of mean length on the X axis (i.e., number of bands) was based on the number of months between size modes and the assumption that one

pair of bands was deposited per year. These two curves were compared visually.

The second source of verification was the analysis of centrum edge type over different seasons. After silver nitrate staining, the centrum edges for all specimens collected in the Monterey Bay area between 1979 and 1981 were characterized as being opaque (highly stained) or translucent (lightly stained). We collected specimens from as many months of the year as possible to detect seasonal variation in the nature of the peripheral band. However, due to the large number of samples taken from the shark derbies, more samples were available in the summer. The number of opaque and translucent edges were plotted by season to assess temporal variation in edge deposition patterns.

The third source of evidence came from the tag-recapture study, which provided size data over a known time increment for individual recaptured sharks, and an oxytetracycline (OTC) mark in each centrum. Between 26 July and 13 September 1979, 948 leopard sharks were collected off Hunters Point in south San Francisco Bay, with a 183 m longline rigged with an average of 150 baited hooks, and fished on the bottom at depths of 15–20 m. Prior to release, TL and PCL were recorded, and each fish was given an interperitoneal injection of OTC at a dosage rate of approximately 25 mg per kg BW, to mark the most recent growth zone in the vertebral centra (Gruber & Stout 1983, Smith 1984). Sex and general physical condition of each fish were recorded and seriously injured fish were not tagged. A plastic tag (Kato & Carvallo 1967) was applied to the first dorsal fin and the shark was released at the capture location. The fin tags were imprinted with a legend that described the reward and recapture processing instructions (Smith 1984).

Every effort was made to obtain accurate measurements and vertebrae from recaptured sharks. If any doubt arose regarding the reliability of a measurement, it was not used. Centra from recaptured sharks were embedded and sectioned (0.5–0.6 mm; Smith 1984) and stored in the dark to prevent loss of OTC fluorescence. Sections were mounted on slides and examined under a dissecting

microscope at 12 or 25 $\times$ magnification, using transmitted substage light alternately with reflected ultraviolet (UV) light to discern the band patterns and numbers in relation to the OTC mark (Smith 1984).

The number of growth zones distal to the OTC mark was plotted against the time, in portions of years, that each shark had been at large. A least-squares linear regression analysis was performed on these data. The null hypothesis that the slope (b) of the relationship between number of bands and time was equal to one, a situation occurring if one opaque and one translucent band were deposited each year, was tested using a two-tailed t test (Zar 1974).

Growth of individual recaptured sharks was plotted against time-at-large on the von Bertalanffy growth curve derived from centrum band counts. Here, the size and estimated age-at-recapture served to place each fish on the curve. The time-at-large determined the distance on the X axis (number of bands), and the size-at-tagging determined the slope. These lines were compared visually with the size-at-age data from the centrum readings.

In addition, average growth rate (cm year⁻¹) was calculated for tagged sharks at liberty for one or more years. When these growth increments are plotted against the length-at-capture, the slope provides an independent estimate of K, and the intercept is an independent estimate of the asymptotic length, L_{∞} (Gulland 1983). There are at least two assumptions necessary to use this technique: (1) growth rates based on varying time intervals are representative of growth over the entire time interval (in our data set, years-at-large averaged 3.8 yr and ranged from 1 to 8 yr); and (2) the relationship between growth rate and length-at-capture is linear and statistically significant.

We also used length and time-at-large to provide information on the growth of the tagged portion of the population. In this approach, the age-at-recapture and the difference between capture and recapture lengths were used in two computer programs that estimate parameters of the VBGF. The first was a von Bertalanffy subroutine of the curve-fitting program FISHPARM (Prager et al. 1987), which uses length-at-age data. The second was the

program BGC4 (by P.K. Tomlinson, in Abramson 1971), which estimates the parameters K and L_{∞} using length-at-tagging, length-at-recapture, and time-at-large. This program fits the equation:

$$l_{t+\Delta t} = l_t e^{-K\Delta t} + L_{\infty}(1 - e^{-K\Delta t}); K > 0,$$

where l_t is the length at tagging, $l_{t+\Delta t}$ is the length at recapture, and Δt is time-at-large. The third parameter, t_0 , cannot be estimated using tag-recapture data alone.

Results from these two programs were compared with those from the other techniques. The growth coefficient (K) and asymptotic length (L_{∞}) calculated from growth in the field were compared to the equivalent values from the age- and length-at-recapture length data. If our age estimates and length measurements at time of tagging are accurate, both values should be similar.

In addition, growth curves obtained from observed growth of the NMFS tagged sample and untagged central California sample were compared to discern possible effects of tagging and/or OTC injection on growth. Because the tagged sample represented only fish of an intermediate size, the growth curve was generated using only fish within the size range of those aged recaptures in the NMFS study (610–1220 mm TL). To facilitate a visual comparison of the two curves, the BGC4 curve, which only describes growth in TL over annual increments and not by age, was situated along the X axis by positioning the starting length of the curve (610 mm TL) at a band count (estimated age) of 3.5 yr, which is the average we obtained for fish of this size aged from vertebrae.

Using the reproductive information obtained from dissected specimens, the size and estimated age at which male and female leopard sharks mature was assessed. For males, clasper length (CL) was plotted against TL, and the length at which CL began to rapidly rise provided an indication of first maturity. Presence of active spermatozoa and coiling of the vas deferens were used to further categorize sharks and were compared with size and age estimates. Similarly, female sexual maturity was demonstrated when the width and degree of vascularization of female oviducts indicated either re-

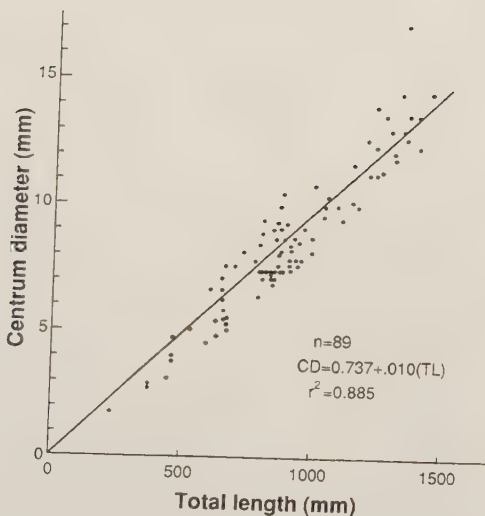


Fig. 2. Relationship between total length (TL) and centrum diameter (CD) of the leopard shark, with sexes combined.

cent birth or embryo abortion, or the oviducts contained fertilized eggs or embryos.

Results

The relationship between TL of the shark and centrum diameter was linear and significant (Fig. 2; $r^2 = 0.89$, $p < 0.001$). Thus, the centra grew proportionately to shark length over all size classes sampled, making this structure useful for age analysis. Ages were estimated using vertebral centra from 85 male and 77 female leopard sharks collected in central California. These sharks ranged from 226 to 1450 mm TL, and had from 0 to 24 bands. The largest shark was estimated to be 19 years old and the oldest shark (24 bands) was a male of 1364 mm TL.

Precision of band counts was relatively high between two readers (Fig. 3). D and APE were 4.9% and percent agreement within ± 2 yr was 90.7%. This set of comparative readings included specimens of widely ranging sizes and age estimates (from 5 to 24 yr). Thus, the error measured was most likely due to difficulties defining criteria among widely varied numbers, sizes, and spacing

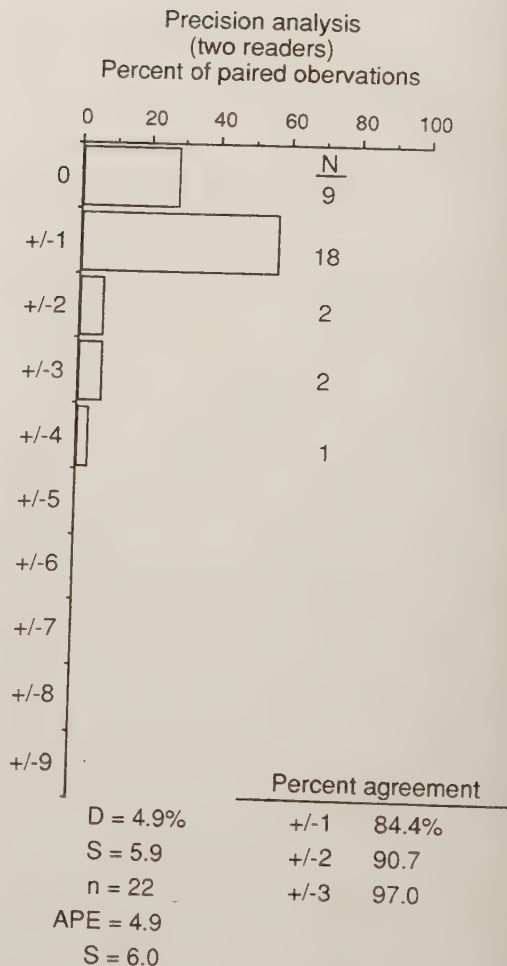


Fig. 3. Precision of age estimate of the leopard shark, with both sexes combined. Histogram represents the difference (as the percent of paired band counts differing by 1, 2, 3, etc. years) between two readers. The proportion of counts which agreed within a certain number of band counts is listed under 'percent agreement', and D, APE, and S are percent error, average percent error, and their standard deviations, respectively (Beamish & Fournier 1981, Chang 1982). The letter n represents the number of samples (centra) aged during this comparison, while N is the number of comparative readings of those centra.

of growth bands. However, because percent agreement was high and usually within 2 years or less, a consensus was always reached.

The VBGC determined for combined sexes of leopard shark had a growth coefficient (K: Ricker

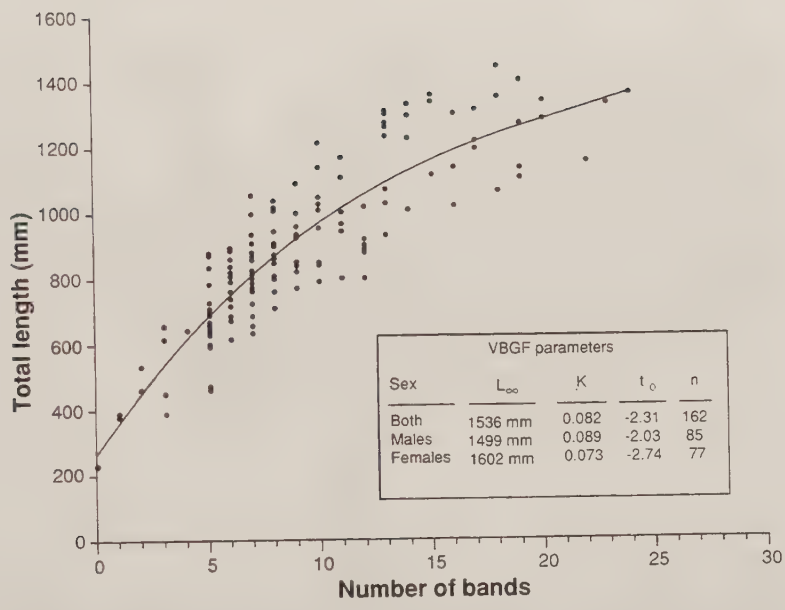


Fig. 4. Von Bertalanffy growth function (VBGF) for 162 leopard sharks of both sexes, collected in central California waters, in which the number of bands was estimated using the silver nitrate staining and thin-sectioning technique on vertebral centra. VBGF parameters and sample sizes for combined and separate sexes are given in the insert.

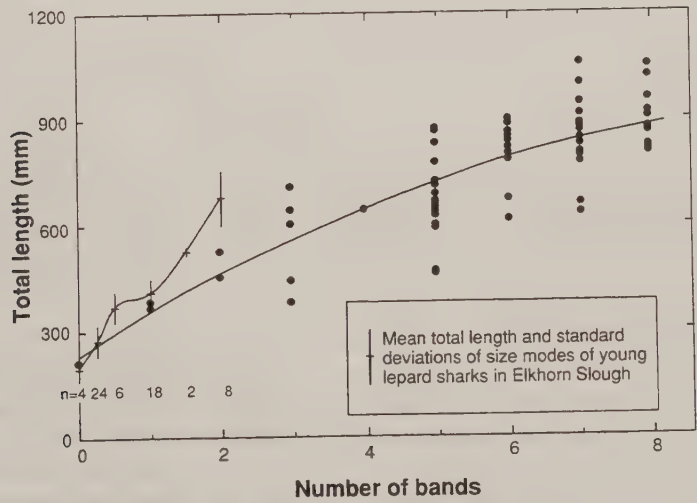


Fig. 5. Growth of young-of-the-year (YOY) leopard sharks, with a line connecting mean length of size modes during the first two years. VBGF for the first 4 years is plotted for comparison. Data for YOY sharks are taken from collections between 1979 and 1981 in Elkhorn Slough (Barry 1983).

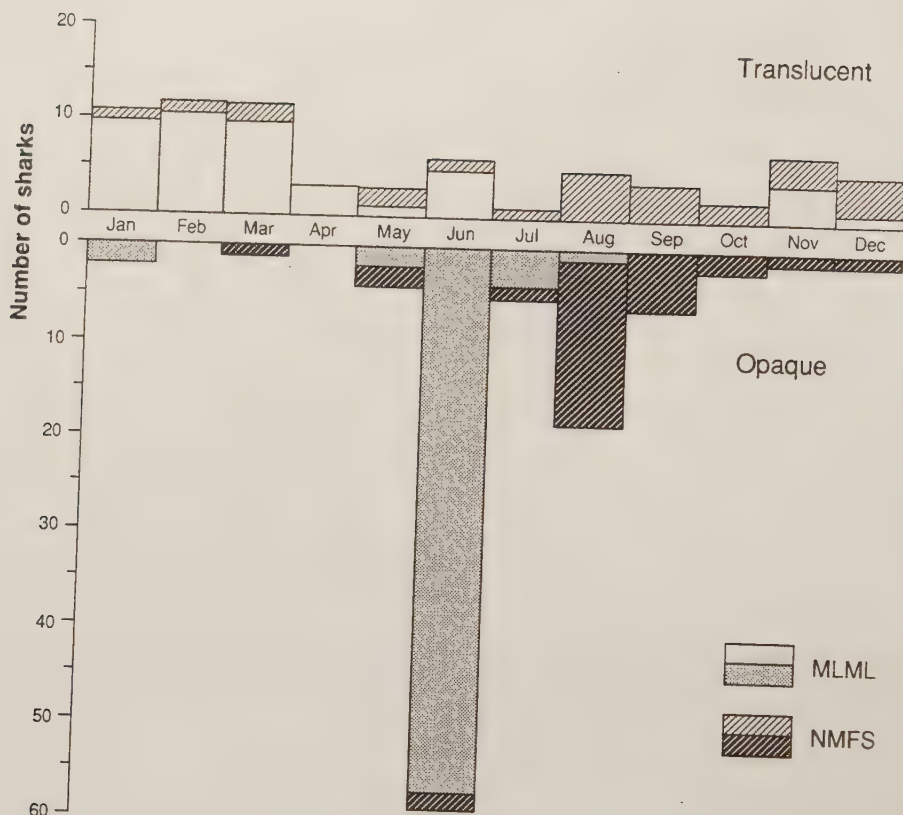


Fig. 6. Centrum edge characteristics by month, with seasonal alternation of peripheral zones from opaque in summer months to translucent in winter months. Those sharks taken from Monterey Bay and Elkhorn Slough are labelled 'MLML', and those taken from San Francisco Bay are labelled 'NMFS'.

1975) of 0.082 and produced a curve that steadily approached the calculated asymptotic length (L_{∞}) of 1536 mm (Fig. 4). This curve appeared to closely match the observed data, judging from the low standard errors of 102.5 mm for L_{∞} and 0.014 for K . The asymptotic length was less than the maximum reported size of leopard sharks (1981 mm TL: Miller & Lea 1972), but was close to the maximum size of those collected in Elkhorn Slough (1515 mm TL: Ackerman 1971). The size at 0 bands was approximately 260 mm TL, which agrees with known size-at-birth (Ackerman 1971). The estimated age at zero size (t_0) was -2.31 yr, a figure which could be partly of statistical rather than biological significance.

The VBGF parameters, determined for separate

sexes, suggest that females ($n = 77$) attain a slightly larger asymptotic TL ($L_{\infty} = 1602$ mm) than males ($n = 85$; $L_{\infty} = 1499$ mm TL), but that males grow faster ($K = 0.089$) than females ($K = 0.073$). However, these differences were not statistically significant.

Size mode analysis of YOY leopard sharks collected monthly in Elkhorn Slough produced a growth trend which was similar to that determined from band counts during the first year, but which was faster than the VBGF during the second year (Fig. 5). Numerous problems arise when interpreting such modal trends, including delineation of modes, emigration of year classes, differential growth of individuals, and underrepresented sizes in the samples. However, it appears that modal

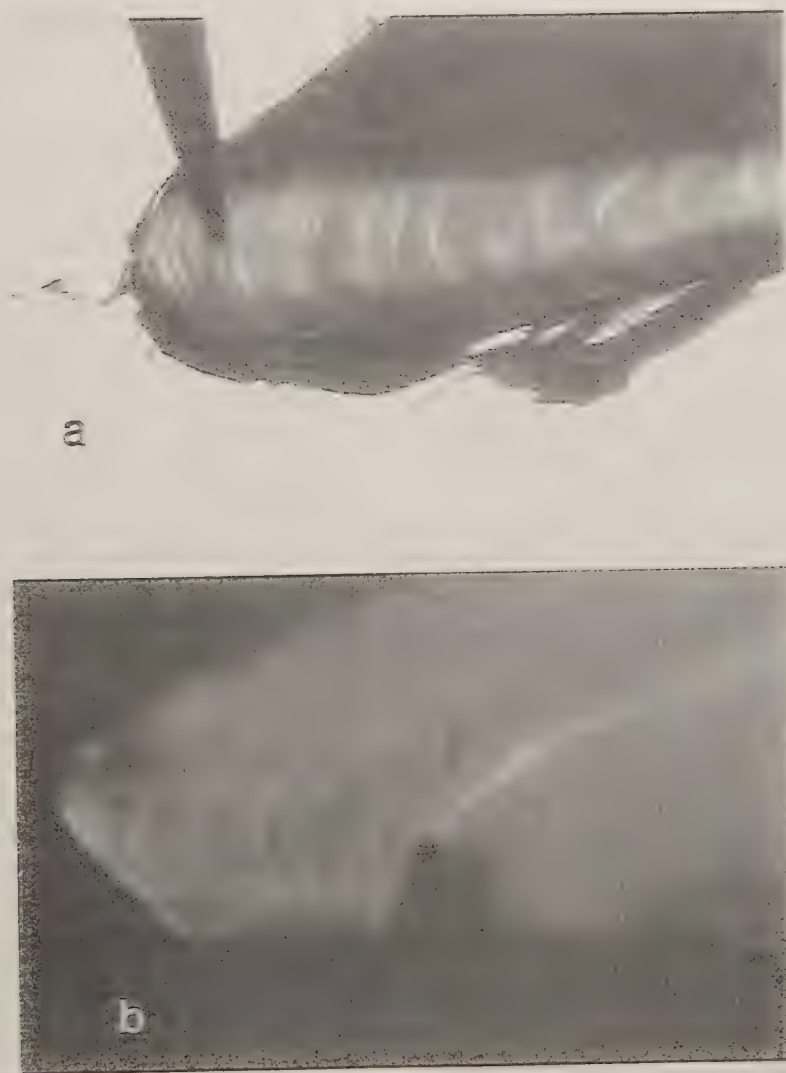


Fig. 7. OTC marks (pointer) and two typical band patterns outside these marked bands in the thin section of leopard shark centra: a – 4 relatively narrow bands distal to the OTC mark, from specimen # 497, a male shark that grew from 108 to 111 mm TL in 4.8 years and was estimated to be 19 years old at recapture; b – 7 relatively broad bands distal to the OTC mark, from specimen # 280, a female that grew from 98.6 to 122 mm in 7.3 years and was estimated to be 17 years old at recapture. The photographs were produced using : a – transmitted incandescent illumination; and b – ultraviolet light alone.

analysis agrees with band counts for the first year of the leopard shark's life, and supports the annual periodicity of growth band deposition in vertebral centra of YOY sharks.

The nature of the peripheral zone on the cen-

trum edge varied predictably with season (Fig. 6). Opaque peripheral bands occurred mainly on centra from sharks captured in late spring through summer, while translucent peripheral bands primarily occurred in centra from sharks collected

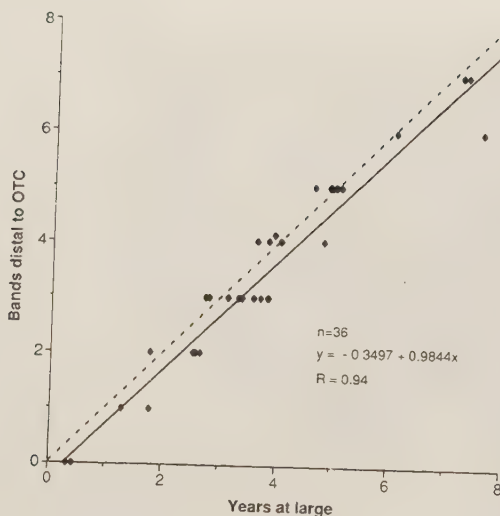


Fig. 8. Number of band counts distal to the OTC mark versus the number of years the specimen was at large. This relationship is significant and linear ($r = 0.94$, $p >>> 0.001$), and had a slope which was not statistically different from one ($p <<< 0.001$; Zar 1974). The dotted line represents a perfect 1:1 relationship with a slope of 1.0 and the solid line is the one that fits the data.

mostly in fall and winter months. From the 116 specimens collected in Monterey and San Francisco Bays, 67 had opaque edges while 49 had translucent ones.

There were 104 tagged sharks recaptured in the 8 yrs after tagging. From these, 51 vertebral samples were obtained for ageing. Reliable growth information (i.e., length at tagging and recapture) was available for 61 specimens, of which 56 were at liberty for one year or more. Sufficient OTC uptake was found in 36 specimens, allowing a reading of the number of bands distal to the OTC mark and a comparison with time-at-large. The male:female ratio of recaptures was 53:47, exactly the same as that at tagging.

Two general patterns of zone formation were noted (Fig. 7). In the first pattern, a group of relatively narrow bands were obvious outside of the OTC mark (Fig. 7a). The second pattern consisted of more widely spaced bands (Fig. 7b). These patterns were generally associated with the relatively slow or fast growth, respectively, of the individual shark.

There was a significant, linear correlation between the number of bands distal to the OTC and the number of years at large (Fig. 8; $r = 0.94$; $n =$

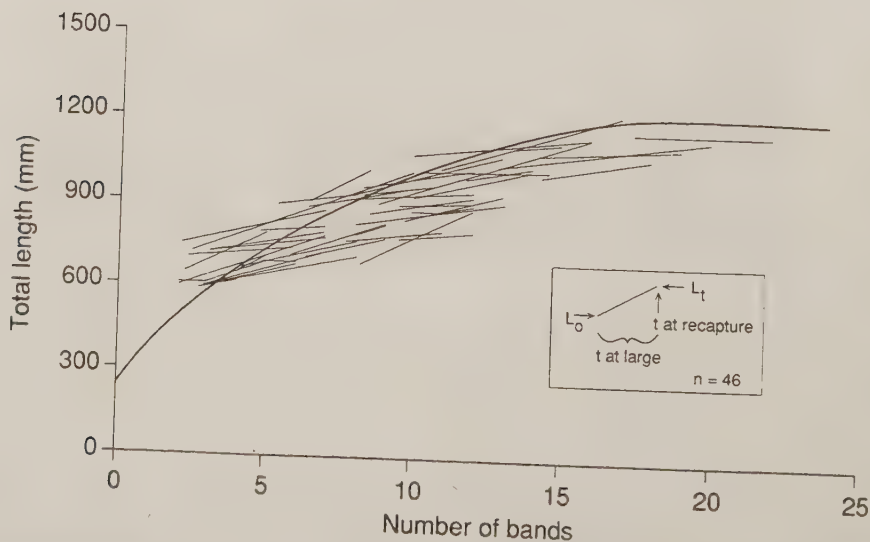


Fig. 9. Growth of 46 tagged and recaptured male and female leopard sharks. Each line is the result of tag-recapture information on size, age at recapture, and time at large from sharks tagged in San Francisco Bay by Smith (1984).

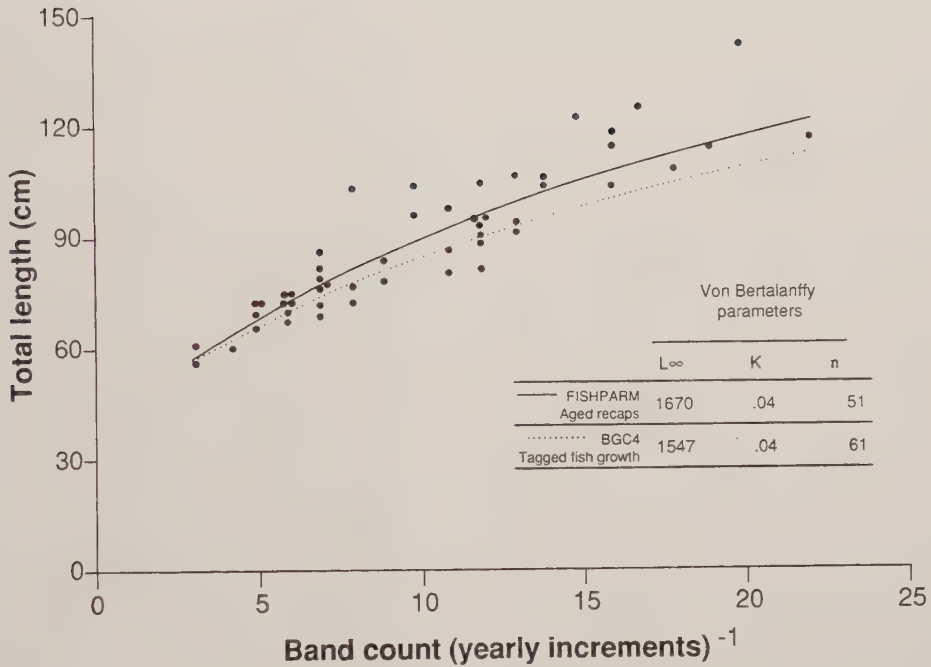


Fig. 10. VBGFs generated from vertebral band count and length of leopard shark at time of recapture (FISHPARM: solid line), and from interim growth of sharks between tagging and recapture (BGC4: dashed line).

36; $p \gg 0.001$). Time-at-large prior to recapture ranged from 0.32 to 7.6 years, and the number of bands distal to the OTC mark ranged from 0 to 7, for specimens which ranged in size from 59 to 116 cm TL at time of original capture. The observed slope of this relationship ($b = 0.984$) was not significantly different from the expected value of 1 ($p \gg 0.001$). These results confirm the hypothesis that one pair of vertebral growth bands is produced per year in this species.

Changes in TL of the 46 leopard sharks for which there were lengths at capture and recapture, time-at-large, and age estimates, corresponded well with the growth curve generated by the VBGF from centrum band counts (Fig. 9). Individual growth rates and time-at-large varied a great deal, but the majority of individual growth lines had slopes which closely approximated the curve.

There was considerable variation in average annual growth rate (cm yr^{-1}) among the 56 recaptured fish at liberty for 1 year or more, resulting in a

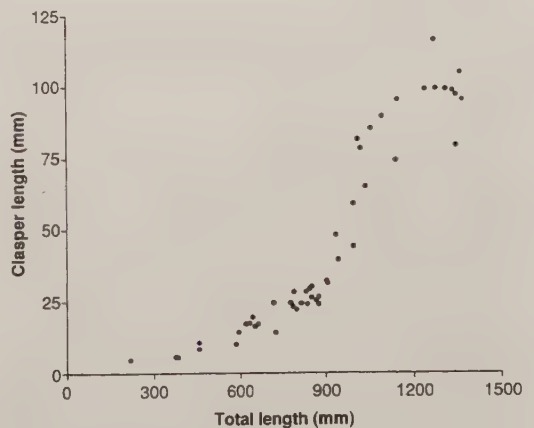


Fig. 11. Relationship of clasper length (CL) to total length (TL). The abrupt increase in CL between 1000 mm and 1200 mm TL coincides with maturation of spermatozoa and vas deferens of 16 specimens.

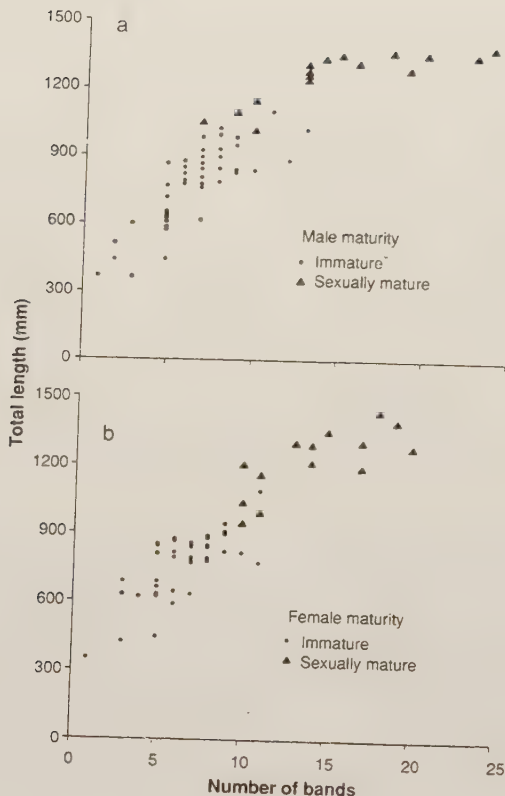


Fig. 12. Length-at-age estimates and sexual maturity information for separate sexes of leopard sharks. Maturity designation given in insert: a – male maturity was based upon developmental status of claspers, presence of mature spermatozoa, and coiling of the vas deferens; b – female maturity was based upon the developmental status of ovaries and oviducts.

statistically insignificant correlation coefficient between annual growth rate and length at capture (cm). Because of this variability, predicted by Sainsbury (1980), Gulland's (1983) annual incremental growth technique, when applied to the leopard shark growth data, was inappropriate. It is interesting, however, that the larger sharks tended to have slower annual growth rates and that the asymptotic length and growth coefficient values predicted by this method ($L_{\infty} = 1508$ cm TL, and $K = 0.029$, respectively) compared favorably with estimates using other methods.

Three of the recaptured sharks did not grow at all, 27 grew between 0.1 – 2.0 cm yr^{-1} , 21 between

2.1 – 4.0 cm yr^{-1} , while only 5 grew more than 4.1 cm yr^{-1} . The overall average annual growth rate was 2.14 cm yr^{-1} , with females averaging 2.3 (range 0 – 5.9 ; $n = 32$), and males averaging 2.0 cm yr^{-1} (range 0.2 – 4.9 ; $n = 24$).

The VBGFs calculated from (1) aged sharks and length-at-recapture using FISHPARM, and from (2) interim growth of tagged and recaptured sharks only using BGC4, produced growth curves and parameters which were very similar (Fig. 10). The values for K (0.04) obtained by the two methods were identical, indicating strong agreement between observed growth and growth calculated from estimated age-at-length alone. However, these K values were only half of those produced from the age-at-length analysis of the entire data set (Fig. 4: $K = 0.082$), indicating that growth of tagged fish might be slower. The values for L_{∞} (1670 and 1547 cm TL, respectively) were also similar, both to each other and to those produced by the entire data set (Fig. 4; $L_{\infty} = 1536$ mm TL). These apparent differences were not statistically significant due to the large standard errors associated with K and L_{∞} values from both data sets.

Length and age of leopard sharks at time of sexual maturation differed only slightly between sexes. Males first become mature at approximately 1000 mm TL as evidenced by the rapid increase in CL at that size (Fig. 11), the maturation of spermatozoa identified in sperm smears of 16 sharks, and the subsequent development of the vas deferens in all specimens over 1000 mm TL. The youngest mature male in our sample had 7 vertebral bands (Fig. 12a). The oldest and largest male in our sample was 1364 mm TL and had 24 bands. In contrast, the youngest male was 226 mm TL but had 0 bands.

Females attained maturity at approximately 1050 mm TL (Fig. 12b). The oldest, but not largest, female in our sample was 1290 mm TL and had 20 bands, while the youngest was 375 mm TL and had one band. The youngest mature female in our sample had 10 vertebral bands. At TLs greater than 1100 mm, all females collected showed signs of either recent birth or embryo abortion (based upon width and degree of vascularization of oviducts), or were pregnant, with oviducts containing embryos.

Discussion

In this study, several independent methods of processing vertebral centra and counting band pairs produced very similar results within specific size ranges, thus satisfying the criteria defined by Wilson et al. (1983). In addition, the precision analysis (Fig. 3) concluded that percent agreement was high and error low. Indeed, our D and APE values (4.9) were considerably lower than those found in equivalent age precision analyses on *Mustelus manazo*, another triakid species which is more difficult to age (Cailliet et al. 1990: D = 6.8–8.9) and on *Prionace glauca*, a carcharhinid species in which reader and sample processing technique caused high variability in counts (Tanaka et al. 1990: D = 6.1–21.9).

The growth of elasmobranch skeletons has been considered to be a determinate process of deposition, in which no resorption of minerals occurs (Applegate 1967, Simkiss 1974, Cailliet et al. 1983a). The significant correlation found between TL and CL (Fig. 2) supports this contention, and agrees with Tanaka & Mizue's (1971) and Taniuchi et al.'s (1983) studies of *Mustelus manazo*. The variability found in this relationship may, however, be related to resorption of minerals in small amounts or at variable times in the life of the shark. Indeed, radioisotope composition in different parts of the centra of four elasmobranch species, including the leopard shark, was not useful in assessing growth; this was attributed to a violation of the assumption of no resorption of minerals (Welden et al. 1987).

The age and size data for leopard sharks fit the von Bertalanffy growth equation well. However, computation of VBGF parameters for combined and separate sexes (Fig. 4) resulted in asymptotic TL estimates that were well below the maximum observed length (1981 mm TL; Miller & Lea 1972). These discrepancies may be attributable to the lack of specimens greater than 1450 mm TL, a problem similar to that of Tanaka & Mizue (1971) in their study of *Mustelus manazo*. The goodness of fit of data to the VBGF can seriously influence the growth model parameters obtained (Cailliet et al. 1990). Individual leopard sharks rarely attain the

maximum size. In fact, most adults are smaller than 1600 mm TL (Compagno 1984). Also, the asymptotic TL is not necessarily the largest recorded, but rather represents the mean size of the oldest group of fish.

The VBGF asymptotic length was slightly higher for females, yet the growth coefficient was higher for males (Fig. 4), suggesting that females may get larger but grow more slowly, a situation commonly found in other species of sharks (Compagno 1984). However, a larger sample size, with better representation of all size classes, is necessary before this question can be adequately assessed statistically (Cailliet & Tanaka 1990).

For the leopard sharks in this study, the growth coefficient (K) was 0.082 for combined sexes, a value below the range of 0.1 to 0.2 predicted by Holden (1974) from ratios of length at birth to maximum observed length. However, Holden (1974) had assumed a gestation period of two years for *Triakis barboursi*, which is considerably longer than the commonly assumed gestation period of 10–12 months for *Triakis semifasciata* in California (Ackerman 1971, Smith & Abramson 1990). The estimated gestation periods of seven species of the triakid genus *Mustelus* range from 10–13 months in duration with corresponding K values between 0.22 and 0.53, based upon extrapolation from embryonic growth (Francis 1981).

Mean sizes of modes of YOY leopard sharks provide a standard by which to compare mean sizes predicted by growth curves derived from band counts (Fig. 5). The greatest agreement between predicted and observed sizes occurred among smaller, younger sharks, because they are born in predictable habitats, are easier to sample, and there is less variation in size-at-age in these younger individuals than in older ones (Ackerman 1971, Cailliet et al. 1983a, 1986). Model analysis indicated a slightly faster growth rate in the second year than that predicted by the VBGF. This could be explained if more than one age class was included in this larger size mode. One additional explanation for this difference in growth rates could be the lack of small specimens in our sample of centra, thus negatively influencing the accuracy of our early growth estimates from size mode analysis.

However, Ackerman's (1971) analysis of YOY size frequencies was based upon a larger sample and resulted in identical estimates of mean sizes of the first four year classes.

The seasonal variation in centrum edge characteristics of the leopard sharks also supported the annual band formation hypothesis (Fig. 6; see also Smith 1984). Vertebrae from sharks captured from June through August generally had opaque edges, while sharks captured from November through April had non-stained, translucent edges. It is unknown whether the opaque zones contain more calcium and phosphate, as in the spiny dogfish (*Squalus acanthias*; Jones & Geen 1977b), and the common thresher (*Alopias vulpinus*) and gray reef (*Carcharhinus amblyrhynchos*) sharks (Cailliet & Radtke 1987). From the centrum edges of three species of *Mustelus*, one pair of translucent and opaque bands was discerned for each year, therefore supporting annual deposition (Tanaka & Mizue 1971, Yudin & Cailliet 1990). The marginal band may be obscured by connective tissue (Holden & Vince 1973, Roussouw 1984, Smith 1984). However, techniques used in the present study provided easily discernible edges for observation.

Seasonal and annual variation in the deposition of the material in the centrum edges are influenced by changes in food consumption and availability, environmental factors, or endogenous growth rhythms that differentially affect uptake of elements from water (Jones & Geen 1977b), and exchange of calcium between the circulatory and skeletal system (Welden et al. 1987). It is difficult to determine which of these factors influence the centrum edge formation in the leopard shark.

Many studies of field-tagged and recaptured elasmobranchs have reported growth information (for reviews, see Cailliet et al. 1986, Cailliet 1990), but often this growth information is not related to vertebral band counts. We were able to obtain such information, because reliable data on interim growth were available for 94% of our sharks aged at recapture.

The occurrence of two patterns of band deposition (Fig. 7) and the relationship of these patterns with body growth (Fig. 6, 8) indicate that there is a relationship between the number, width, spacing,

and opacity of bands and body growth. These two patterns also were described in spine sections for the spiny dogfish from a recent tag-recapture study (Beamish & McFarlane 1985, McFarlane & Beamish 1987).

The rates of growth that were derived from changes in body size over known periods of time (Fig. 9) also indicate that the growth equation derived from age estimates of centra is accurate. While some sharks did not grow at all, and others grew more slowly or faster, most of them grew approximately as the VBGF model predicted. Inaccurate measurements could have accounted for some of the discrepancies between observed and predicted growth rates. Fish growth could also have been influenced by capture handling, tagging, and OTC injection.

The most likely explanation of any discrepancies between individual growth rate and that estimated by the VBGF is that growth rates vary considerably with response to environmental conditions. High individual growth variation is not unusual in sharks (Thorson & Lacy 1982), and was noted in two populations of *Mustelus manazo* (Tanaka & Mizue 1971, Taniuchi et al. 1983, Cailliet et al. 1990). Growth rates of individual tagged slit-eye sharks (*Carcharhinus albomarginatus*, now *Loxodon macrorhinus*; Compagno 1984) of almost identical lengths ranged from -23 cm to $+20.8$ cm year⁻¹ (Kato & Carvallo 1967). Captive *Heterodontus portusjacksoni* exhibited extreme variation in growth rates (McLaughlin & O'Gower 1971). Age at length also varied widely for *Galeorhinus japonicus* (Tanaka et al. 1978) and *Prionace glauca* (Cailliet et al. 1983b, Tanaka et al. 1990).

We have demonstrated that the stained and sectional vertebral centra of leopard sharks offer a good method for growth analysis. In addition, we have provided convincing verification and validation to support the hypothesis that centrum bands are annually deposited (Smith 1984). This evidence ranges from size frequency analysis of YOY, to seasonal centrum edge analysis and tag-recapture and OTC-marked growth data from the field.

Our data support the hypothesis that leopard sharks, like many elasmobranchs, exhibit late maturation (Fig. 11, 12). Females were observed to

mature at ages between 10 and 15 years, 1050 to 1350 mm TL, and 0.72 to 0.93, respectively of their asymptotic length. Males mature between 7 and 13 years, 1000 to 1050 mm TL and 0.63 to 0.66 of their asymptotic length. These values are slightly lower than Ackerman's (1971), in which the smallest mature female was 1180 mm TL, but normal size of maturity was around 1200 mm TL. *Galeorhinus zyopterus* matures after 9 years (Holden 1977) and *Squalus acanthias* matures after 14–23 years (Ketchen 1972, 1975, Holden 1973, Jones & Geen 1977a), or longer (Beamish & McFarlane 1983). All of these estimates agree with Holden's (1974) suggestion that female elasmobranchs, in general, attain sexual maturity at 0.6–0.9 of their asymptotic length. In contrast, male elasmobranchs mature at a smaller size than females (Hisaw & Abramowitz 1938, Springer & Lowe 1963, Teshima et al. 1971, Tanaka & Mizue 1971, Francis & Mace 1980), as evidenced by rapid increase in CL (Clark & von Schmidt 1965).

The leopard shark has a relatively slow growth rate, matures relatively late in life, and has a low fecundity of 7–36 offspring per female during each year-long reproductive season (Ackerman 1971). An estimated longevity of 25–30 years (Smith 1984), however, is considerably higher than the 13–16 years suggested by Ackerman (1971) from size frequency analysis. All of these life history features contribute to the suggestion that they are susceptible to over-exploitation.

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Planning Models for Individual Transferable Quota Programs¹

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Lanfersieck, J., and D. Squires. 1992. Planning models for individual transferable quota programs. *Can. J. Fish. Aquat. Sci.* 49: 2313–2321.

This paper develops an approach to simulating markets for individual transferable quotas prior to their actual implementation. This approach is based on linear programming models for individual vessels that allow estimation of market derived demand for quota to simulate the expected equilibrium market price for quota and maximum quasi-rents for alternative quota allocations. The simulated price is an annual lease or rental price. The approach, applied to a sample of longline vessels targeting sablefish (*Anoplopoma fimbria*) in the Columbia INPFC area of the United States, indicates substantial potential gain in quasi-rent and economic efficiency from quota trade. The simulated quota exchange also indicates potential for concentration of quota. The quota market risks becoming thin, noisy, and hampered by noncompetitive forces, potentially requiring limits to quota transfer and concentration.

Le présent article élabore une approche pour la simulation des marchés des quotas individuels transférables avant leur mise en oeuvre réelle. L'approche est basée sur des modèles de programmation linéaire pour les navires individuels qui permettent d'estimer la demande du marché en quotas afin de simuler le prix d'équilibre du marché prévu pour le quota et les quasi-rentes maximales pour les autres allocations de quotas possibles. Le prix simulé est un prix de crédit-bail ou de location annuel. L'approche, appliquée à un échantillon de palangriers pêchant la morue charbonnière (*Anoplopoma fimbria*) dans le secteur INPFC Columbia aux États-Unis, indique un gain potentiel substantiel en matière de quasi-rentes et d'efficacité économique découlant du commerce des quotas. La simulation des échanges de quotas indique également un potentiel de concentration des quotas. Le marché des quotas risque de devenir faible, tumultueux et entravé par des forces non concurrentielles, ce qui pourrait nécessiter l'imposition de limites au transfert et à la concentration des quotas.

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1. Introduction

Individual transferable quotas (ITQs) are tradable property rights over the flow of the resource stock (Scott 1986). Each vessel is allocated a quantity of the total harvest for which it has a right to catch over some time period. ITQs are now earning the attention of fishery managers worldwide as a means to regulate common property fishing industries (Muse and Schelle 1989).

Several fundamental issues concern regulators and industry when planning or considering the feasibility of an ITQ program. First is the expected equilibrium price and economic rents (total revenue less the payment required to bring into production an input fixed in supply). A second concern is the gains in economic efficiency from quota trade.³ Third, regulators are concerned about potential quota and industry concentration and competitiveness as well as thinness (number of participants) of the quota market. Resolution of these sources of uncertainty

would enable better evaluation and planning of prospective ITQ programs.

This paper is expository, with several purposes. First, the paper aims to facilitate transfer of information from economics to fisheries management. Second, the paper develops a simulation model of an ITQ market based on linear programming models for individual vessels that can address the above concerns about a proposed ITQ program while it is still in the planning stages. Third, the simulation model estimates economic benefits from a potential ITQ program in a longline fishery for sablefish (*Anoplopoma fimbria*) off Oregon and Washington in the United States and estimates the expected price of quotas for alternative allocations among vessels. The efficiency gains from quota trade and expected equilibrium ITQ price from the simulation model are short-run, since they are conditional upon the existing vessels; Squires et al. (1992) addressed the expected entry/exit of vessels and industry structure of the fleet. The simulated price is an annual lease or rental price.

The paper proceeds as follows. Section two discusses important features of an economic model of ITQs and a survey of the relevant modeling literature, ITQ price formation, background information on the longline fishery for sablefish, a linear programming model to estimate the vessel's short-run production technology and unit quota rents, which form the basis of the simulation, and short-run equilibrium price formation of the ITQ and expected quasi-rents and gains from trade. Section three reports empirical results from the simulation model and discusses policy implications for an ITQ management program.

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³Gains from trade, i.e. arbitrage efficiency, due to production are the increase in value of output (producer surplus) that occurs due to trade between producers. This exchange allows producers to specialize according to their comparative efficiencies. Gains from trade can also include consumption gains (consumer surplus). Only producer gains are considered because output prices are assumed constant in this paper.

2. Materials and Methods

2.1. Features of an Economic Model for ITQs and Literature Review

The economic model of ITQs rests upon the foundation initially developed in the environmental pollution (Dales 1968; Baumol and Oates 1971; Montgomery 1972; Weitzman 1974) and international trade (Anderson 1988) literatures and extended by Christy (1973) and Moloney and Pearce (1979) to fisheries. This framework builds upon the individual firm (vessel), explicitly recognizing that the market for ITQs is formed by individual firms exchanging quota. This paper uses firm and vessel interchangeably but recognizes that some firms may be multivessel.

The fisheries literature on ITQs (Christy 1973; Moloney and Pearce 1979; Copes 1986; Scott 1986; Lindner et al. 1989; Muse and Schelle 1989; Sissenwine and Pace 1992) has not fully recognized two other important points. The first (Lau 1976) recognizes that the vessel's (firm's) production decisions are made in two steps. In the first step, the vessel maximizes profits (total revenue less operating costs) in the short term from the existing capital stock (vessel and equipment). (These short-run profits are also called quasi-rents or producer surplus; see Just et al. 1982.) In the second step, the vessel adjusts, over a longer time period, its capital stock (e.g. change vessels) to the appropriate size to maximize long-run profits.

The second point (Schulze and d'Arge 1974) is that both short- and long-run economic efficiency have two requirements when controlling an externality (a cost external to the vessel but which affects other vessels in the fishery, such as the abundance of fish in open-access fisheries). The first requirement is that the marginal value of the vessel's output must equal marginal cost (both internal and external to the vessel). The second requirement is that the total value of the vessel's output must not be less than total costs (both internal and external to the vessel).

Taken together, these points imply that a single, long-run equilibrium ITQ price does not immediately develop. Instead, equilibrium ITQ prices form over short-run periods as individual vessels exchange quota. Over a longer time period, vessels evaluate all revenues and costs, including the expected ITQ price and their implicit marginal valuation of their capital stock, and then adjust their capital stock or technology by changing vessel size, gear, or electronics, or by leaving the industry. New participants may also enter the industry. Although beyond the scope of this paper, it is also possible that changes in industry structure may change fish stock biomass and production costs, which will induce additional changes in the industry.

An ITQ price subsequently forms for the corresponding long-run equilibrium structure of the fleet. This price includes the user cost of the unpriced resource given the existing fleet size and structure and an optimally set quota (Moloney and Pearce 1979). The user cost of the resource is the opportunity cost to the user of taking a unit of the resource in the present period and represents the shadow price of the fish stock (Clark 1976). This long-run price is the present value of the net returns from this asset.

The vessel's investment and entry/exit decision and long-term ITQ price formation can take varied lengths of time. In the Australian bluefin tuna (*Thunnus thynnus*) and U.S. surf clam (*Spisula solidissima*) fisheries, industry restructuring proceeded fairly rapidly, while the process has been protracted

in New Zealand (Geen and Nayer 1989; Lindner et al. 1989; Campbell 1990; Anonymous 1991).

In sum, economic models of ITQs should recognize that ITQ markets are formed by individual vessels (firms) exchanging quota and that different ITQ prices exist for different periods.

The issue of competitive equilibrium market prices must also be addressed by simulation models of ITQ markets. Hahn (1984) and Misiolek and Elder (1989) examined non-competitiveness or monopoly power in the market for tradable property rights over pollution, and Anderson (1991) extended the analysis to fisheries. When simulating the initial, short-run ITQ price for the existing fleet, lack of market competitiveness from a small number of participants may not necessarily pose a problem, since quota is typically allocated amongst an overcapitalized fleet with excessive vessel numbers. Also, evaluating the vessels' investment and entry/exit decisions and likelihood for quota trade sheds light upon this issue.

The paper's simulation generates a single competitive equilibrium price for ITQs, but in practice one may not form. Lindner et al. (1989) and Lindner (1990) found evidence of considerable price dispersion (widely distributed prices rather than a single equilibrium price) and sequential, bilateral exchange in New Zealand. Nonetheless, simulating the expected equilibrium ITQ price for the existing fleet provides the best possible estimate of the expected price and also a basis for comparing alternative policies.

Empirical studies of ITQs in fisheries have only recently emerged. Geen and Nayer (1989) assessed ITQs in a retrospective or ex post framework for the Australian bluefin tuna. Their industry-wide bioeconomic model generated the long-run equilibrium price of quota and industry structure. Geen et al. (1990) applied linear programming to assess a priori a program of individual quotas in the multispecies southeast trawl fishery in Australia. Individual quotas could not be explicitly transferred in the model and the effects of quota trading on adjustments in production were incorporated into the model indirectly. Hence, this model primarily focused upon the long-run effects of investment and industry restructuring under ITQs. Haynes and Pascoe (1988), in a linear programming study of the northern prawn (*Pandalus borealis*) fishery of Australia, noted that the results of an industry-level model correspond to a sole owner (solving the incomplete property rights structure of a common property fishery, thereby alleviating the stock effect externality) and hence give a theoretically identical result to that from a program of ITQs. This approach, while theoretically correct, assumes a common, single (aggregate) production technology for each vessel grouping. Most importantly, this approach does not allow fully analyzing the likely operation of the ITQ market to assess the hypothetical competitive equilibrium market price, resource rents (total revenue less costs), gains in efficiency from trade, and distribution of the licenses and trade patterns.

Squires (1990, 1991), following the two-step procedure above, simulated a potential ITQ program for trawlers. The expected short-run equilibrium ITQ price was estimated and the effect of the ITQ price upon the individual vessel's investment or disinvestment decision assessed. Econometric studies, such as this one, suffer from the possible failure of the model to be well behaved and from its parametric form, i.e. an explicit functional form must be imposed on the data. The econometric approach can handle statistical noise, but it imposes an explicit and possibly overly restrictive functional form for the production technology.

An alternative vessel-level approach is possible, drawing from the study of production efficiency in the economics literature (Lovell and Schmidt 1988). One strand of this literature circumvents the parametric assumptions of the econometric approach by representing each individual firm's production as a separate linear programming problem. Hence, studies of prospective ITQ markets can specify a linear program for each vessel, impose quota and calculate the unit quota rent, use this price (unit rent) – quantity relationship to simulate the ITQ market, and determine the ITQ's expected equilibrium price. This study develops this framework in a prototype procedure, adapting the empirical approaches of Hahn and Noll (1983), Anderson (1988), and Squires (1991) to linear programming to give the expected annual lease or rental price under certainty.

The deterministic qualities of the linear programming approach circumvent many econometric problems, but linear programming has limitations of its own. Linear programming imposes constant returns to scale (a 1% increase in inputs increases output by 1%), fixed proportions among outputs (Leontief technology), and nonjointness-in-inputs (separate production processes for each output or groups of outputs). Moreover, because of the linearity, profitable activities are employed subject solely to resource constraints rather than diminishing returns (e.g. rising operating costs as search time increases) and changing prices. Hence: (1) calibration of the model to observed production is difficult without adding a number of additional, ad hoc constraints and (2) large changes in the solution (basis) are often observed for small changes in the constraints, prices, or technical coefficients.

Other linear programming studies of fisheries include Brown et al. (1979), Siegel et al. (1979), Meuriot and Gates (1983), Overholtz (1985), Huppert and Squires (1987), Haynes and Pascoe (1988), and Geen et al. (1990).

2.2. ITQ Price Formation

After the allocation of quota but prior to its exchange, each unit (e.g. pound, percentage) of the quota has an implicit economic value or unit economic rent. For the profit-maximizing vessel, this unit rent τ , is the vessel's unit quasi-rent (producer surplus). That is, τ is the difference between the marginal revenue from production P (the increase in total revenue for a one-unit increase in output) and the vessel's marginal cost (MC, the increase in cost for a one-unit increase in output), i.e. $\tau = P - MC$. (With joint production, the quota's virtual price replaces marginal cost (Squires and Kirkley 1991). Virtual prices are those prices which would induce an unconstrained firm to behave in the same manner as when faced with a given vector of quantity constraints; see Neary and Roberts (1980) for further discussion.)

For a single year, τ is conditional upon the capital stock (vessel and equipment) and short-run marginal costs and is equivalent to the price of annual lease or rental quota measured as a quasi-rent (Campbell 1990). Over a longer period, when capital (vessel, equipment) has time to adjust, τ becomes the net present value of the expected net earnings stream, i.e. $\tau = \sum_t (P_t - LMC_t) / (1 + \delta)^t$, where δ is the discount rate, $t = 1, \dots, T$, T is the planning horizon, LMC_t is expected long-run marginal cost (marginal cost when all inputs can vary) in time t , and P_t is the expected output price in time t .

This unit quota rent τ varies among firms according to the output and input prices they face and their marginal costs (which are determined by their production technology and prices for inputs such as fuel and labor). The important point here is that

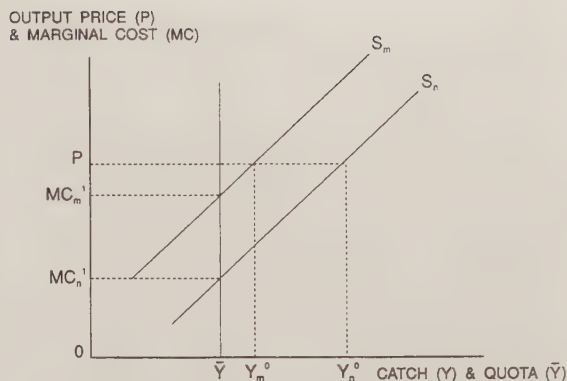


FIG. 1. Quota market for two vessels.

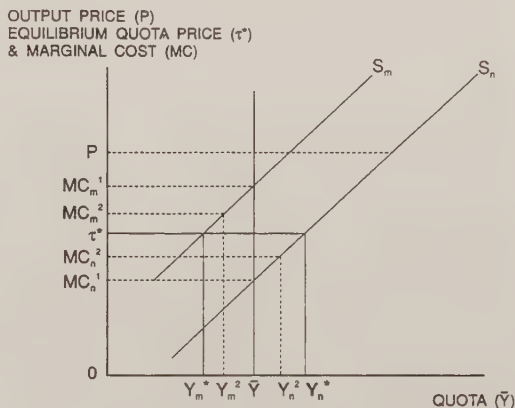


FIG. 2. Quota exchange process.

for exogenous and fixed output prices, the most efficient vessel (with lowest marginal costs) will place a higher value on a unit of quota than an inefficient one, i.e. $\tau_n > \tau_m$ because $MC_n < MC_m$. Consequently, a vessel n will demand quota from (supply to) firm m when $\tau_n > (<) \tau_m$. While the price paid for these species is constant and determined exogenously, MC varies with the level of quota held, so that quota purchase (sale) monotonically lowers (raises) τ in the quota market until an equilibrium market price for quota τ^* is formed and the value of a unit quota is the same for all vessels ($\tau_n = \tau_m$) at the last unit exchanged.

Figure 1 (Squires 1990) illustrates the quota market for two vessels m and n . The supply curve (equal to marginal cost and reflecting diminishing returns in this example) for vessel m lies above that for vessel n , indicating that vessel n is more efficient, i.e. can produce any given output level at lower cost. Prior to quota, both vessels face the same exogenous price for fish P , and vessel n (m) produces Y_n^0 (Y_m^0). Under a quota of $\bar{Y}$, vessel n (m) faces marginal cost MC_n (MC_m). Hence, $\tau_n = P - MC_n > \tau_m = P - MC_m$ and vessel n will buy quota from vessel m .

Figure 2 illustrates how quota exchange progressively narrows τ between vessels, until unit quota rents are equalized at the last unit traded, i.e. $\tau_m = \tau_n$, and the equilibrium ITQ price τ^* is formed. Initially, each vessel faces market price P and catches Y_m^0 and Y_n^0 (not shown). Each vessel is subsequently

allocated $\bar{Y}$ and faces a unit quota rent of $\tau_m = P - MC_m^1$ or $\tau_n = P - MC_n^1$. Vessel m sells quota to vessel n , since $\tau_m < \tau_n$, causing τ_m to rise and τ_n to fall, reaching an intermediate position such as $P - MC_m^2$ and $P - MC_n^2$ with quota holdings Y_m^2 and Y_n^2 . Trade continues until the unit quota rents are equalized for the last unit of quota exchanged, giving final quota holdings of Y_m^* and Y_n^* . In this two-vessel example, vessel n 's final purchase ($\bar{Y} - Y_n^*$) equals that sold by vessel m (Y_m^*).

The efficient outcome after competitive exchange of quota is given by equalizing the net returns from holding quota, τ , across all N vessels in the industry, i.e. $\tau_1 = \tau_2 = \dots = \tau_N = \tau^*$. In practice, τ^* differs between vessels by an amount equal to costs from transactions, information, transportation, risk, and uncertainty (these amounts vary by vessel).

Quota exchange amongst vessels gives gains from trade due to reduction in production costs (also called arbitrage efficiency). Economic rents from the species are maximized and gains from trade are enjoyed as less efficient vessels trade quota to more efficient vessels. The full economic rent generated by the resource, $\tau^* \bar{Y}$, where $\bar{Y}$ is the overall industry quota for the species, is also the revenue government receives if quota were initially auctioned at a single price or were placed under a uniform tax (Weitzman 1974; Anderson 1988). In theory, at least, the initial distribution of quota only affects the distribution of rents among vessels, not the efficiency after exchange (Montgomery 1972). If $\bar{Y}$ is optimal, then the equilibrium quota price formed after exchange, τ^* , is the marginal user cost of the unit resource (Moloney and Pearce 1979).

When linear programming is used to model the firm's short-run production technology (i.e. capital is fixed), short-run marginal costs (SMC) equal average variable costs (AVC) because of the constant returns to scale (a 1% increase in inputs yields a 1% increase in output) assumed in a linear programming model. Assuming competitive and exogenous prices, $\tau = P - SMC = P - AVC$. The unit quota rent prior to exchange τ , i.e. the firm's implicit marginal valuation of quota, is given with linear programming models by the shadow value of the quota constraint (the increase in profit with a one unit increase in the quota constraint). That is, the linear program measures the value of a unit quota to a vessel by estimating the change in a vessel's profits for an additional unit of quota. If Z denotes the vessel's short-run profits and $\bar{y}$ is the vessel's allocated quota, then $\tau = \delta Z / \delta \bar{y}$, where δ is partial derivative. The gains in net revenue with a one unit increase in $\bar{y}$ include net revenue gains from bycatch as well as from the regulated species because vessels can catch more of other species.

2.3. Sablefish Longliners of Columbia INPFC Area

The ITQ simulation was applied to the Columbia management region, which runs from Cape Blanco, Oregon (43°00'N), to Cape Elizabeth, Washington (47°30'N). The region's ports include Coos Bay, Waldport, Newport, Tillamook, Astoria, and Portland in Oregon and Ilwaco and Westport in Washington. The relatively small number of ports makes the Columbia region an easy area in which to monitor landings, which would be important in an ITQ program.

Fixed gear (longline and fish pot) and groundfish trawl operators in the Pacific sablefish fleet dispute the allocation of allowable sablefish harvest, with fixed gear and trawl vessel groups each desiring a larger share. Strong Japanese sablefish demand for U.S. exports supports high ex-vessel prices of sablefish, further elevating the gear conflict in the sablefish fleet. These factors, the limited number of ports, longevity, and

relative stability of recruitment to the sablefish biomass (which results in stable resource supply), make it a potential species for a market-based solution to the allocation issue.

2.4. Empirical Model

The linear programming model for the Columbia sablefish fishery is a modified version of that employed by Huppert and Squires (1987) to estimate the optimal size of the Pacific coast trawl fleet. The model maximizes the vessel's short-run profit (quasi-rent or producer surplus; Just et al. 1982), conditional upon the vessel or capital stock, subject to constraints on total allowable annual harvest and on vessel-weeks fished and the standard nonnegativity constraints (no variable is negative). The decision variable for each vessel is the number of weeks fished W_j in each quarter j ($j = 1, 2, 3, 4$) of the year, i.e. vessels vary weeks fished to maximize quasi-rent (short-run profits). The model is specified for each vessel as

$$(1) \max Z = \sum_i \sum_j W_j (P_{ij} a_{ij} - VC_s)$$

W_j

subject to

$$(2) \sum_j W_j a_{ij} \leq y_i \quad \text{for all } i,$$

$$(3) W_j \leq 10 \quad \text{for all } j,$$

$$(4) \sum_j W_j \leq \bar{W},$$

and

$$(5) W_j \geq 0 \quad \text{for all } j.$$

Quasi-rent for each vessel, Z , is total revenue less variable costs. The exogenous ex-vessel price for species $i = 1, \dots, 18$ in quarter j is denoted P_{ij} . Variable cost per week for vessel size class s ($s = 1, \dots, 5$), VC_s , is the short-run (operating) costs per week per vessel. The technical coefficients, a_{ij} , are weekly catch rates, i.e. tons of species i harvested per week by the vessel in quarter j . Each vessel's production limit for species i is denoted y_i . If the vessel is subject to quota, then for species i , $\bar{y}_i$ indicates the quota level for the individual vessel.

The first constraint, equation (2), represents the annual limits on each vessel's catch of species i . The second constraint, equation (3), constrains the harvesting activity of a longliner to 10 wk in a quarter. The third constraint, equation (4), is an annual constraint which requires the optimum annual sum of weeks fished by each vessel to not exceed the actual annual weeks fished $\bar{W}$. The actual weeks fished was less than the annual constraint of 40 wk implied by equation (3). The fourth constraint, equation (5), represents the standard nonnegativity constraint for the decision variable, weeks fished (W_j).

The 18 species potentially harvested by vessels are Dover sole (*Microstomus pacificus*), English sole (*Pleuronectes vetulus*), petrale sole (*Eopsetta jordani*), Pacific halibut (*Hippoglossus stenolepis*), other flatfish, lingcod (*Ophiodon elongatus*), Pacific cod (*Gadus macrocephalus*), Pacific hake (*Merluccius productus*), Pacific ocean perch (*Sebastes alutus*), widow rockfish (*Sebastes entomelas*), yellowtail rockfish (*Sebastes flavidus*), shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*Sebastolobus altivelis*), other rockfish, salmon, albacore, shrimp, crab, and a group of other miscellaneous species. Over the course of the year, most vessels tend to concentrate production upon sablefish and some combination of halibut, lingcod, and rockfish.

The liner programming approach to optimizing the vessel's short-run profit is conditional upon existing vessel size, vintage (age), and state of technology (electronics, design, etc.). The underlying bioeconomic model is one of certainty and short-run static equilibrium. Hence, fish prices and input prices are assumed fixed and exogenously determined, fish stock densities and harvest rates do not depend upon the level of harvest, and the harvesting technology is constant (Huppert and Squires 1987).

These assumptions are reasonable for a vessel-level model of a region, since prices are determined coastwide over all gear types. Moreover, sablefish and thornyhead prices are likely to be exogenously determined in the Tokyo wholesale market (current research is addressing this issue). Dockside fuel prices are set by a standard mark-up procedure following the terminal price in Seattle or San Francisco. Some variation is observed coastwide, reflecting differences in marketing margins and perhaps product form and quality and competitiveness of the market structure.

Finally, the model does not consider the costs of management or optimal level of resource use. Instead, the optimal level of each ITQ-managed species, in this case only sablefish, is exogenously determined. Solving the long-run optimal level would require solution of each firm's long-run optimum level of capital stock, the optimum aggregate capital in the industry, and optimal abundance level.

2.5. Data and Variable Construction

A total of 139 longliners operated in the Pacific coast ground-fish fishery in 1987 (PacFIN Research Data Base), of which 105 landed at least 0.5 metric ton of sablefish in the Columbia area (PacFIN Research Data Base). From these 105 vessels, the top 30 revenue producers or "highliners" were selected to insure individual vessels in the model covered their short-run costs and to simplify the modeling process.

Five size classes of vessels were selected for the study: (1) ≤ 15.0 m, (2) 15.1–16.0 m, (3) 16.1–18.0 m, (4) 18.1–20.0 m, and (5) ≥ 20.1 m. The size composition of the sample fleet, based on U.S. Coast Guard registered length, generally reflected the Pacific longline fleet. The number of vessels in each class was (1) 14, (2) 5, (3) 5, (4) 4, and (5) 2.

Highliners in Columbia landed approximately 20% of the sablefish landed coastwide by longliners during 1987 (Natural Resources Consultants 1988). The Columbia landings include multispecies catch (2519.52 metric tons) valued at \$4.1 million (1987 U.S. dollars), consisting mainly of sablefish (889.87 metric tons) valued at \$1.3 million. The mean ex-vessel price per metric ton for sablefish was \$1606.30, which was higher than the coastwide 1987 ex-vessel price of \$1040.00.

Technical coefficients a_{ij} were computed as weekly average catches (in metric tons) by quarter for each vessel from the 1987 PacFIN Research Data Base. Each "week" of fishing represents one calendar week in which at least one commercial landing was recorded. Week was selected rather than trip, since larger vessels make longer but fewer trips than smaller vessels and the latter may make several trips in a week. The choice of trip tends to otherwise overstate the time fished of smaller vessels.

Quarterly species prices were quarterly ex-vessel arithmetic means from the PacFIN Research Data Base. Variable costs included the costs of fuel, oil, provisions, ice, bait, gear replacement, crew, and bonuses. The labor costs were observed costs rather than estimates of opportunity costs. These cost data were obtained from a random sample survey of coastwide

sablefish longline and fish pot vessels for 1987. Median rather than mean variable costs were computed because of the skewed and relatively limited sample size for each vessel size class.

2.6. Quota Allocation

Six different levels of overall quota $\bar{Y}$ were allocated among the 30 vessels for the simulation. The first overall quota was set at the total metric tons harvested by the sample of Columbia sablefish longliners in 1987. Subsequent industry sablefish quotas in the model were set at 90, 80, 70, 60, and 50% of the initial industry quota. Each vessel was allocated quota in proportion to its share of the actual catch in 1987 as a percentage of the target level, rather than in absolute units. In the model, quota is assumed issued without charge, to be freely transferable, and sufficiently divisible so that the small denominations and large numbers contribute to an active and competitive market in quota. The problem considers a certain and static environment and does not allow banking of quota for future use.

2.7. Derived Demand for Sablefish Quota

Demand curves show quantity demanded of a commodity as a function of its price and other exogenous factors. Inverse demand curves show price as a function of quantity demanded and the other exogenous factors.

Vessels have a derived demand for quota. That is, given ex-vessel fish prices and technology, the vessel's demand curve for quota is derived from final demand for that species and the vessel's costs and production technology (Squires 1990, 1991). To estimate the derived demand for quota used in the simulation model of the ITQ market, the linear programming model is first run to obtain estimates of the unit quota rent τ (which are the shadow prices for different vessel quotas $\bar{y}$). The vessel's inverse derived demand for the sablefish quota is then estimated by regressing τ upon the vessel's quota ($\bar{y}$) and dummy variables (D_s) for different vessel size classes, where the intercept α_0 represents the smallest vessels:

$$(6) \quad \tau = \alpha_0 + \sum_{s=2}^5 \alpha_s D_s + \beta \bar{y}.$$

Ordinary least squares estimates are potentially biased because τ is censored at zero. That is, not all vessels are bound by quota, so that the shadow value derived from the linear programming model can be zero. In such instances, Tobin's censored regression technique is appropriate (Maddala 1985).

2.8. Equilibrium Market Quota Price

The estimated inverse derived demands for individual vessels, from equation (6), were summed over the N (30) vessels to get the inverse market-derived demand curve for an overall quota $\bar{Y}$:

$$(7) \quad \tau^* = \alpha_0 + \frac{1}{N} \sum_{j=2}^N \sum_{s=2}^5 \alpha_s D_s + \frac{1}{N} \beta \bar{Y}.$$

The equilibrium market price for quota in the short run, τ^* , conditional upon the existing fleet capital stock, is the price that clears the ITQ market (the price for which demand equals supply) for the given, fixed supply of industry quota, $\bar{Y}$. This price is equivalent to that of an auction market or an optimal tax (Anderson 1988) and implicitly assumes that all units of quota are exchanged on the market. Thus, τ^* was determined

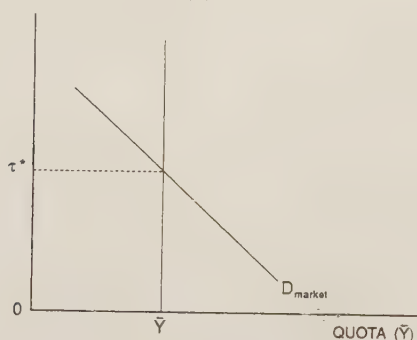
MARKET EQUILIBRIUM ITQ PRICE (τ^*)

FIG. 3. Equilibrium market price for individual transferable quotas.

by evaluating equation (7) at $\bar{Y}$ ($= \sum \bar{Y}_i$). This aggregate quota $\bar{Y}$ forms the vertical (perfectly inelastic) sablefish industry quota supply curve. Figure 3 illustrates the market for one quota allocation. Six different values for τ^* were obtained, one for each $\bar{Y}$.

Shadow values from the linear programming model represent the value to the firm of an additional unit of output, including the value of the additional landed bycatch made available by relaxing the binding quota constraint. Hence, the market equilibrium price for sablefish quota can be greater than the ex-vessel sablefish price because τ incorporates the vessel's revenues from bycatch. Sample vessels were selected based upon minimum annual landings of 0.5 metric ton of sablefish rather than on a per trip basis. Some trips may have targeted more upon sablefish than other species. Hence, the contribution of bycatch to the unit rent of the sablefish quota, τ , may be overstated by the model.

2.9. Gains from Trade

Industry gains from trade are the difference between the industry rent after trade and the total industry rent before trade (but after the quota allocation), assuming all sablefish rents are valued in τ^* . Industry rent gains occur when vessels trade quota allocations $\bar{y}_i$, each vessel adjusting production and quota holdings to maximize quasi-rents (also called producer surplus or short-run profits; see Just et al. 1982). The total industry rent after trade is the area under the market demand curve for quota up to $\bar{Y}$. Given the linear demand curve, this area is $\tau^* \bar{Y} + 0.5[\alpha_0 + 1/N \sum \alpha_i D_i - \tau^*] \bar{Y} = 0.5[\tau^* + \alpha_0 + 1/N \sum \alpha_i D_i] \bar{Y}$. The total industry gains from trade at the competitive equilibrium market price, τ^* , are $0.5[\tau^* + \alpha_0 + 1/N \sum \alpha_i D_i] \bar{Y} - 0.5 \sum [\tau + \alpha_0 + 1/N \sum \alpha_i D_i] \bar{y}_i$ (summing over all vessels for each of the six aggregate quotas $\bar{Y}$).

3. Empirical Results and Discussion

The linear programming model was run for the six different quota allocations for each of the 30 vessels. The subsequent data generated for the simulation were six sets of τ - $\bar{y}$ pairs for the 30 vessels. Equation (6), the firm's inverse demand for quota, was then estimated by Tobit analysis as discussed in Section 2.7.

3.1. Inverse Demand for Quota

The statistical significance of the vessel size class dummies in equation (6) was assessed by a log-likelihood test. The like-

TABLE 1. Parameter estimates of vessel inverse demand curve for quota. An asterisk indicates statistically significant at 2%. Intercept is smallest vessel size class. Tobit analysis, giving maximum likelihood estimates. Log-likelihood = -1485.5.

Variable	Coefficient	t-ratio	Significance
Constant	3308.16*	2.579	0.9911
Size two dummy	-2731.54	-1.261	0.8038
Size three dummy	-991.264	-0.486	0.4838
Size four dummy	-788.081	-0.352	0.3866
Size five dummy	38628.4*	13.150	1.00
Quota	-66.214*	-2.229	0.9853

TABLE 2. Equilibrium quota market price flexibilities.

Quota allocation	Price flexibility
Initial allocation	-0.24279
90% of initial	-0.20902
80% of initial	-0.19248
70% of initial	-0.18644
60% of initial	-0.18633
50% of initial	-0.18565

lihood ratio test statistic for all dummy variables was 123.4 for four independent restrictions, indicating that the null hypothesis of no differences in unit rents among size classes could be rejected at the 0.01 level of significance. The three midsized vessel size classes have negative coefficients for the dummy variables; these coefficients were not individually statistically significant from zero but were as a group, since the chi-square statistic was 113.0 for three restrictions. Hence, the full model including all vessel size classes was retained (Table 1).

The positive sign of the statistically significant coefficients for the largest and smallest size classes indicated that these vessels have the largest unit quota rents τ (prior to exchange). The negative signs for the midsized vessels indicate inefficiency compared with the smallest and largest. Hence, the largest vessels, and possibly the smallest, should have the largest unit quota rents τ and purchase quota from the midsized vessels selling quota.

3.2. Elasticity of Market Demand for Quota

The price flexibility of τ^* , $\delta \ln \tau^* / \delta \ln \bar{Y}$, indicates the percentage change in equilibrium quota prices τ^* for a 1% change in the overall quota, $\bar{Y}$, i.e. the sensitivity of τ^* to changes in quota $\bar{Y}$. The estimated price flexibilities are inelastic, which means that a 1% increase in quota reduces τ^* by less than 1%, in this case 0.24%. Extreme short-run price variability is not expected. The price flexibility declines with tighter quotas (Table 2). An inelastic price flexibility is consistent with an elastic demand (Tomek and Robinson 1981), so that an increase in the ITQ market price by greater than 1% causes a greater than 1% decline in ITQ quantity demanded. Hence, market demand for quota is elastic.

An elastic market demand for quota suggests that total resource rents inversely vary with the level of quota, but that these proportional changes in resource rents are less than the proportional change in the aggregate quota. Hence, the fishery's economic rent can be maintained at nearly the same level over a broad range of overall quotas. This result should facilitate resource conservation, since conservative quotas could be used without a large opportunity cost of rent foregone. This suggests a conservative strategy that simultaneously protects the resource stock and insulates the industry against abrupt and

large reductions in the overall quota if new stock assessments show a sudden population decline or that previous resource assessments were in error (Squires 1991).

3.3. Equilibrium ITQ Market Price

The market equilibrium prices for the sablefish ITQ, τ^* , conditional upon the existing fleet structure and vessel sizes, are reported in Table 3 for the six alternative levels of industry quota, $\bar{Y}$. For the initial allocation, τ^* was \$3193. As expected, τ^* monotonically increased as $\bar{Y}$ decreased, peaking at \$4175.83.

The values of τ^* are relatively high and are also relatively insensitive to the size of the overall quota level (reducing overall quota by 50% resulted in only a 31% increase in equilibrium ITQ price τ^*). The ITQ should generate an important asset value to initial holders of the right, unless the rights are initially auctioned or are taxed (which transfers some or all of the economic rent from the private sector to the public sector). Moreover, the ITQ has the potential to form a barrier to entry into a fishery with otherwise relatively limited capital requirements. It might be advisable to allocate some of the initial quota to crewmembers to allow the traditional upward mobility historically enjoyed.

The value for τ^* includes the gains in quasi-rents from species other than sablefish when the binding sablefish quota is relaxed. That is, when vessels are allowed to catch more sablefish in the model, they also catch more of other species, which also contributes to their revenues. The more efficient vessels are capable of using revenues from these other species to cross-subsidize purchase of quota. This also lowers unit costs of harvesting all species by spreading out annual fixed costs over greater volume of catch. This then increases overall competitiveness, particularly since much competition is based on output price. Hence, the largest vessels and those with a more diversified harvesting strategy (e.g. they may make targeted rockfish trips) are most likely to trade for quota.

3.4. Economic Rents

The total sablefish rent for the initial allocation of quota, given the capital stock and fleet structure and prior to trade, was \$2.031 million (Table 3). This is the total rent implicit to a nontransferable quota. After exchange, total rent climbed to \$3.138 million, a 67.35% gain from the initial overall quota due to trade and increased efficiency.

The potential size of the rent also suggests ample scope for the public sector to transfer some of the rent from the private sector to the public sector. One possibility is a tax or license fee (Grafton 1992). Auction markets for the initial allocation are also possible.

The proportional gains from trade depend upon the number of vessels exchanging quota. Initially, the most and least efficient vessels trade quota, since between them they enjoy the largest disparities in unit quota rents. Hence, they realize the greatest gains from trade and are least likely to be hampered by the relatively high costs of transactions and information that occur when ITQ markets are rudimentary and thin (few buyers and sellers). When the quota progressively tightened, the proportional gains from trade dropped considerably as the disparity between the efficient and inefficient vessels narrowed.

The results nonetheless indicated substantial gains in efficiency enjoyed through exchange of quota for all quota allocations (Table 3) and the importance of a fully specified property right structure. The relatively large potential rents indicated the size of rent dissipation due to open-access and the potential rents gained through rights-based management. The expected rents may be larger than the regulatory costs of planning, implementing, monitoring, and enforcing an ITQ program for sablefish. A complete cost-benefit analysis of an ITQ program can utilize the projected rents as part of economic benefits.

The reported rents and gains from trade are the maximum possible. In practice, less trade may be observed due to thin markets, private and sequential exchange between vessels rather than all quota exchanged in the ITQ market (all quota are exchanged in the simulation), transactions and information costs, and uncertainty (Noll 1982; Hahn and Noll 1983; Lindner et al. 1989; Lindner 1990; Atkinson and Tietenberg 1991). Markets also take time to form and efficiently operate.

These relatively large gains could reflect large intervessel differences in efficiency, but they may also reflect the relatively extreme solutions often found with linear programming (Shepherd and Garrod 1980). Thus, intervessel efficiency differences may be heightened more with linear models than with models allowing for increasing marginal costs. Also, the potential rents are relatively large because they are short-run and hence exclude costs of capital and other fixed costs (e.g. insurance, moorage).

The results can be compared with the simulation results for a thornyhead transferable quota in the multispecies deepwater trawl fishery in Eureka for 1984 (Squires 1991). The proportional gains from trade in that study were generally less than 10%. The results are a bit difficult to compare because one study depends upon linear programming and maximization of quasi-rents and the other upon econometrics and maximization of revenues.

These results nonetheless suggest that a directed fishery may enjoy greater efficiency gains because of its greater flexibility in the product decision. That is, species mix decisions in a trawl fishery with joint production (multiple outputs produced by a single production process) reflect returns from several species, which must be weighed against one another. Moreover, there may well be lesser scope to alter production, to trade, and to

TABLE 3. Short-run equilibrium quota market price and total quota rent. Gains from trade are industry totals. Equilibrium market price in 1987 U.S. dollars per metric ton. Values estimated conditional upon existing capital stock.

Quota allocation	Market price for quota (\$)	Fleet quota (t)	Total economic rent prior to trade (\$)	Total optimum economic rent (\$)	Gains from trade (\$)	% gain in rent
Initial allocation	3193.79	889.87	2031074	3398956	1367822	67.35
90% of initial	3390.20	800.883	1295791	3137704	1841913	142.15
80% of initial	3586.59	711.906	2183023	2859015	675992	30.97
70% of initial	3783.02	622.909	1998154	2562782	564628	28.26
60% of initial	3979.42	533.922	1733107	2249101	515994	29.77
50% of initial	4175.83	444.935	1494112	1917946	423834	28.37

TABLE 4. Number of quota purchases for alternative quota allocations as a percentage of initial quota holding.

Vessel size class	100%	90%	80%	70%	60%	50%
1 (n = 14)	0	1	1	1	1	1
2 (n = 5)	0	0	0	0	0	2
3 (n = 5)	1	1	1	1	1	1
4 (n = 4)	0	0	1	1	1	1
5 (n = 2)	1	2	2	2	2	2
Total (n = 30)	2	4	5	5	5	7

TABLE 5. Number of quota sales for alternative quota allocations as a percentage of initial quota holding.

Vessel size class	100%	90%	80%	70%	60%	50%
1 (n = 14)	14	13	13	13	13	13
2 (n = 5)	5	5	5	5	5	3
3 (n = 5)	4	4	4	4	4	4
4 (n = 4)	4	4	3	3	3	3
5 (n = 2)	1	0	0	0	0	0
Total (n = 30)	28	26	25	25	25	23

enjoy gains from trade in a trawl fishery than in a directed long-line fishery.

3.5. Concentration of Quota and Limitations to Quota Exchange

In practice, a well-formed price signal τ^* , such as that formed in the simulation, may not develop through extensive quota trade in competitive, well-functioning quota markets. In this case, the price signal does not fully and accurately convey the information for the most efficient resource allocation possible. A competitive market, with large numbers of buyers and sellers who actively trade permits, and a market clearing price do not necessarily develop (Noll 1982; Hahn and Noll 1982; Lindner et al. 1989; Lindner 1990; Atkinson and Tietenberg 1991). Even if the quota market is not concentrated (i.e. quota is not held by relatively few firms), the number of vessels deciding to trade their initial allocation of quota may be too few, the transactions may be strictly sequential, bilateral, and private (i.e. not appearing in the market), uncertainty may be important, or the unit size of quota may be too large, so that transactions are infrequent. In turn, infrequent trades and possibly highly variable price signals can undermine efficient choices of production, investment, and quota exchange and reduce the maximum expected economic rent and arbitrage efficiency. Along these lines, Lindner et al. (1989) and Lindner (1990) reported a widely dispersed price signal, relatively thin markets, and sequential and bilateral ITQ trade in New Zealand and provided a detailed discussion of the likely determinants of quota exchange and market performance.

Tables 4 and 5 report the pattern of quota purchases and sales in the simulation, in which all vessels have exchanged quota. Most vessels sell quota at all allocations, particularly the smallest vessels, and only a few buy, generally the largest vessels.

Vessels that sell quota sell all of it when trade is simulated with a linear model, since the unit quota rent τ is constant over all trade levels. Vessels compare this value τ with the ITQ market equilibrium price τ^* and if $\tau^* > \tau$, they sell all of their quota. In a model with upward sloping supply and marginal cost curves for sablefish, τ progressively declines (grows) as vessels buy (sell) quota. In this case, τ , equalized at the last unit exchanged among all vessels, can occur with vessels trading lesser amounts of quota than with the linear model. Hence,

more balanced trade patterns can be expected. This issue under research.

The simulated quota exchange indicates potential for concentration of quota by only a few vessels. The quota market risks becoming thin, noisy, and hampered by noncompetitive forces, potentially requiring limits to quota transfer and concentration — even when quota is initially allocated through auction markets.

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TUNAS

ALBACORE

History of the Fishery

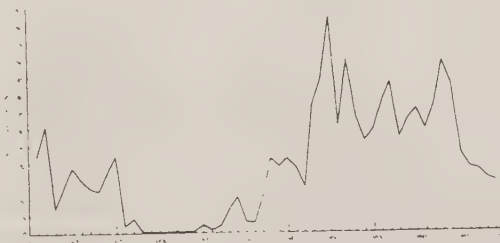
The albacore (*Thunnus alalunga*) is a highly migratory species valuable to commercial and sport fisheries in California. Commercial albacore fishing began off southern California near the turn of this century. In 1903, an experimental pack of 700 cases of albacore led to the development of the U.S. tuna canning industry. The fishery expanded quickly in response to the almost instantaneous high demand for canned tuna, which quickly outpaced the supply of albacore. By the 1920's, bluefin, yellowfin, and skipjack tunas were also being canned. However, albacore is the only tuna species which may be marketed as "white meat tuna," and it brings a premium price at the dock and in the can.

The geographic range of the U.S. north Pacific albacore fishery has expanded during the past eight decades. Early commercial fishermen made one-day trips within coastal waters off southern California. The fishery extended northward and seaward, and by the late 1930's it reached to waters off the Pacific northwest and several hundred miles offshore. There was a major offshore extension in the mid-1970's across the central Pacific to about the Dateline. However, beginning in the mid-1980's, there has been a general shrinking of the breadth of the fishery to within about 500-600 miles of the Pacific west coast.

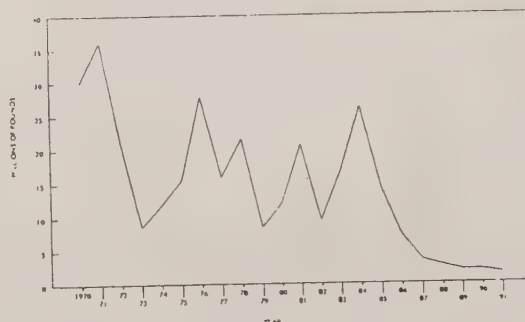
Since the early 1980's, about 90 percent of the annual albacore catch has been made by trolling jigs and 10 percent by live-bait pole-and-line fishing. In earlier years, live-bait fishing sometimes accounted for up to 40 percent of the annual catch. In some years, up to a few hundred tons of albacore may be caught by purse seine vessels, usually incidental to bluefin tuna fishing. California-based drift gillnet vessels also catch small quantities of albacore incidental to shark and swordfish fishing. Generally, two fishermen conduct fishing operations from troll vessels and three to five fishermen from live-bait vessels. Many vessels which fish for albacore also take part in other fisheries. Their participation in the albacore fishery depends on the price and availability of albacore, the success of other fisheries, and weather conditions during the albacore season. In the 1940's, there were about 500 vessels in the albacore fleet. A high of 3,000 boats was reached in 1950; the number dropped to about 1,000 vessels by 1960, climbed to 2,100 vessels during the 1970's, and dropped to fewer than 500 boats in the late 1980's. The average size of albacore jigboats is about 45-50 feet, with a sea-keeping capability of about one to two weeks. In recent years, there has been a steady increase in vessels of 60-80 feet, which are capable of fishing at sea for six to eight weeks. The larger vessels may participate in a virtual year-round albacore fishery by fishing in mid-North Pacific waters, the North American coastal fishery, and in the recently established south Pacific albacore fishery.

The North Pacific albacore stock is also harvested by Asian fisheries, including a Japanese pole-and-line fishery in the

spring, which targets two to five year old fish off the Japanese coast eastward to near the Emperor Seamount chain. There are also Japanese, Taiwanese and South Korean longline fisheries, which target five to seven plus year old albacore in subtropical and temperate waters across much of the Pacific during winter. Beginning in the early 1980's, Asian high-seas drift gillnet fisheries have targeted two to four year old albacore across much of the Pacific. In addition, there is a relatively small Canadian troll fishery for albacore during years when they are distributed in waters off British Columbia.



California commercial landings of albacore, 1916-1969.

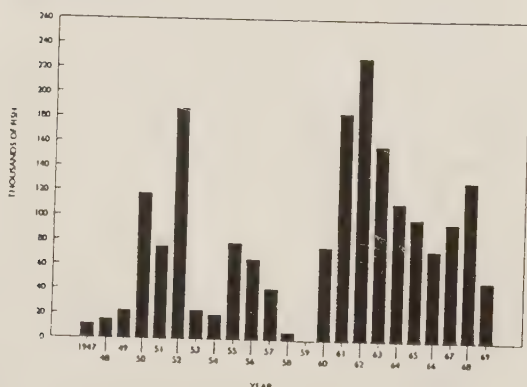


California commercial landings of albacore, 1970-1991.

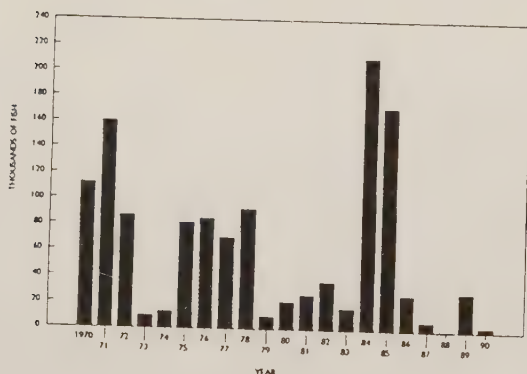
In the late 1890's and early 1900's, sport fishermen on private boats would fish for large bluefin tuna inside the Channel Islands. The 10-20 pound albacore, which would strike the bait intended for a 100 pound bluefin, were considered a nuisance and were usually tossed over the side after landing. Gradually, some boats began to carry sports anglers as paying passengers, who quickly came to appreciate the fighting and eating qualities of the albacore, or "longfin tuna," as they are often called. The fishing for hire partyboats gained in popularity in southern California, and, by the 1950's, about 100-150 fished for albacore in nearshore waters.

In the 1960's, the albacore runs began to shift outside the Channel Islands and to waters off upper Baja California, over 50 miles from southern California ports. In response to this, larger commercial passenger fishing vessels with a greater range were built. Today, there are about 40 large commercial passenger fishing vessels, mostly in southern California and some in the Morro Bay and San Francisco area, that are capable of carrying 20 to 60 sport fishermen on one to three-day fishing

trips. In addition to the large vessels, there are about 50 to 60 smaller vessels that typically are chartered to smaller fishing parties of around six.



California commercial passenger-carrying fishing vessel landings of albacore, 1947-1969.



California commercial passenger-carrying fishing vessel landings of albacore, 1970-1990.

As the result of increased numbers of private boats, the ready availability of modern commercial passenger-carrying fishing vessels (CPFV), and improvements in sport fishing gear, albacore sport fishing has become increasingly attractive to California anglers. In fact, the first albacore of the season caught in southern California waters sets off "albacore fever" among recreational fishermen. No other sport fish in southern California elicits the excitement exhibited each year by the thousands of fishermen pursuing albacore. Over 120,000 anglers go out on southern California CPFVs in search of albacore during the course of a season. Albacore sport fishing in southern California contributes about \$23 million to the local economy through the purchase of the boat ticket, tackle, food, gas, licenses, and lodging.

Status of Biological Knowledge

The albacore is a highly advanced teleost with many specialized adaptations. It is capable of thermoregulation, has a

high metabolic rate, an advanced cardiovascular system, specializations in the circulatory system and blood/gas exchange systems, distinctive enzyme and complement systems, and high energetic costs for migration which may be partly met by utilization of stored fat.



Albacore, *Thunnus alalunga*.

The distribution of albacore is cosmopolitan in subtropical and temperate waters of all oceans. Off the coast of North America, the distribution during summer and fall months may range from lower Baja California, northward to the Queen Charlotte Islands, Canada, and occasionally into the Gulf of Alaska.

There is a growing body of evidence that the North Pacific albacore population is not as homogeneous as is usually assumed. Results from albacore tagging studies suggest that at least two proposed subgroups of fish constitute the North Pacific albacore population and that these subgroups have different migratory patterns, modal sizes in the U.S. fishery, growth rates, and peak spawning periods. While the subgroups are geographically separated and are differentiated by dissimilarities in biological or fishery statistic criteria, they are not believed to be genetically distinct.

Albacore make extensive movements during their lifetime. The degree of migration is geographically most expansive in the pre-adult ages between about two and five years. Fish of these ages may conduct trans-oceanic migrations in temperate and subtropical waters, following well-defined routes between the eastern and western or central Pacific. However, the spawning adults, above about six years, undertake relatively limited movements, mostly within the subtropical and tropical regions of either the western, central or eastern Pacific.

Results from extensive albacore tagging indicate that the northern subgroup of albacore is fished by the U.S. fishery north of about 40°N, the Japanese pole-and-line fishery in the western Pacific, and the Asian longline fishery. The southern subgroup appears to be fished by the U.S. fishery south of about 40°N, and the Asian longline fishery, but only to a limited extent by the Japanese pole-and-line fishery.

Based on physiological research findings, the normal habitat of albacore is within a temperature range of 50°-64° F, with dissolved oxygen saturation greater than about 60 percent. While individuals may temporarily move into waters outside of these values, thermoregulation and respiration functions will be adversely affected and operate marginally. The acoustic tracking of free-swimming albacore has demonstrated that albacore customarily live within the depths of the thermocline, rather than the upper mixed layer as has been generally presumed.

The migration, distribution, availability, and vulnerability of albacore are strongly influenced by oceanographic conditions in the Pacific Ocean, notably oceanic fronts. The seasonal migration of albacore into North American coastal waters is associated with the North Pacific Transition Zone water and its frontal boundaries. In addition, oceanographic conditions also play an important role in the local concentrations and movements of albacore in coastal waters off North America. Albacore tend to aggregate on the warm side of upwelling fronts and move away from the fronts upon their disintegration in response to wind shifts unfavorable for upwelling. Satellite images of ocean color and sea surface temperature and concurrent albacore catch data clearly show that the distribution and availability of albacore off California are related to coastal upwelling fronts and that albacore are most abundant in warm, clear, blue oceanic waters near temperature and color fronts at the seaward edge of coastal water masses.

It is presumed that albacore aggregate in the vicinity of upwelling fronts to feed on small fishes, squids, and crustaceans that are plentiful in these areas. Yet it remains unclear what physical factors prevent albacore from crossing to the cooler side of these fronts in order to reach the highest potential forage biomass. Past beliefs have stressed confinement to a physiological optimum temperature range; however, explanations for environmental preferences of albacore are changing as new knowledge is acquired. The finding that albacore can regulate their body temperatures suggests that temperatures on the cool side of an upwelling front should not be limiting. Studies of free-swimming albacore in relation to ocean thermal structure, using acoustic telemetry and coincident oceanographic sampling, have shown that, while albacore would not cross from the warm side to the cool side of an upwelling front which had a horizontal sea surface temperature gradient of about a 4° F over a few miles, the fish would routinely swim through vertical temperature gradients up to about 18° F. The fish made extensive vertical excursions up to several hundred yards and crossed the thermocline in waters adjacent to the upwelling front. Recent research involving acoustic telemetry of free-swimming albacore, satellite measurements of ocean color and temperature, and oceanographic sampling of water optical and other characteristics, and potential forage abundance, indicates that water clarity as it affects the ability of albacore to detect prey is an important mechanism underlying the aggregation of albacore on the warm, clear sides of upwelling fronts.

Status of Population

Fishing effort and catch of albacore in the Japanese pole-and-line and the U.S. surface fisheries have declined, beginning in the early 1980's. In contrast, recent landings in the Japanese longline fishery have been relatively constant and there has been a rapid development of Asian gillnet fisheries that harvest large numbers of albacore in the North Pacific.

Several factors are associated with the decline in the traditional surface fisheries, but their relative importance is unknown. It appears that no single factor is responsible, but that the decline in catches is a result of complex interactions among factors, including (1) a reduction in overall fishing effort for

albacore, (2) lack of fishing in areas of traditional high catch, (3) indications of population decline and (4) major anomaly patterns in oceanographic conditions across much of the North Pacific in the mid-1980's and early 1990's.

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National Marine Fisheries Service

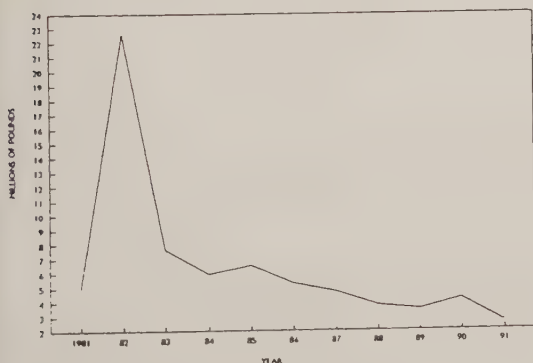
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WIDOW ROCKFISH

History of the Fishery

The widow rockfish (*Sebastes entomelas*) is one of the top three species in commercial landings of rockfish in California and is a minor component of recreational landings. Although there were reports of occasional large trawl catches made incidental to fishing for other species, commercial landings were minor until markets improved in 1979 and midwater trawl fishing began. At this time, fishermen began targeting on the species, and California landings exceeded 10,000 tons by 1982. Since 1983, strict regulations have limited commercial landings. Recent landings are about 1,500 tons. Annual landings are restrained by a quota that applies to the fisheries of California, Oregon and Washington. Trip landings and frequency are also regulated in order to maintain a long open season. Widow rockfish comprise about 60 percent of the commercial rockfish landings in Eureka, 35 percent in Crescent City, and 25 percent in Bodega Bay; they occur as smaller proportions of landings as far south as Santa Barbara. Most widow rockfish are filleted and marketed as Pacific red snapper or rockcod. The landed value approached \$1,000,000 in 1989. Widow rockfish are mostly caught by trawlers. Before the advent of restrictive trip landing limits, most of the fish were caught with large midwater trawls. It can be difficult to avoid capturing more widow rockfish in a single tow with a midwater trawl than trip limits allow, and many vessels are now using only the less efficient bottom trawls. Widow rockfish are also captured with gill nets and longlines.



California commercial landings of widow rockfish, 1981-1991.

Status of Biological Knowledge

Widow rockfish are found from Todos Santos Bay, Baja California, to Kodiak Island, Alaska. Peak abundance is off northern Oregon and southern Washington, with significant aggregations occurring south to central California. While many commercial catches occur at bottom depths between 450 and 750 feet, young fish occur near the surface in shallow waters, and adults have been caught over bottom depths to 1,200 feet. Widow rockfish often form midwater schools, usually at night, over bottom features such as ridges or large mounds near the shelf break. The schooling behavior of widow rockfish is quite

dynamic and probably related to feeding and oceanographic conditions. There appears to be some seasonal movement of fish among adjacent grounds, and there is evidence that fish move from area to area as they age, with fish of the same size staying together.



Widow rockfish, *Sebastes entomelas*.

The maximum recorded age for widow rockfish is 59 years, but fish older than 30 years are uncommon. Most are less than 21 inches in length, which corresponds to a weight of about 4.7 pounds. The maximum size is 24 inches or about 7.3 pounds. At first, growth is fairly rapid and by age five widow rockfish average 13.4 inches. By age 15 growth has slowed, and the average size is 18.7 inches for females and 17.6 inches for males. About 50 percent of widow rockfish are mature by age five, and almost all are mature by age eight when they are 16.6 inches. Off California, fecundity ranged from 55,600 eggs for a 12.8-inch female to 915,200 eggs for a 18.8-inch fish. The release of larvae by widow rockfish peaks in January-February and appears to occur in the same areas where they are caught during that season. The larvae are about 0.2 inch when released. The young fish lead a pelagic existence until they are about five months old. During the latter part of the pelagic stage, the two-inch fish feed mostly on copepods and small stages of euphausiids. Adult widow rockfish feed on midwater prey such as lantern fish, small Pacific whiting, euphausiids, sergestid (deep water) shrimp, and salps. Juvenile rockfish, including widow rockfish, are important prey items for sea birds and chinook salmon in May and June. Little is known about predation on adult widow rockfish.

Status of Population

The population was virtually unfished prior to 1979. By 1982, it became obvious that the population was being rapidly fished down and would soon be overfished, if catches were not restricted. The fishery was placed under stringent regulations in 1983. The population is now estimated to be at about the level chosen by management to maintain a viable spawning stock. The 1991 quota is 7,700 tons for the combined landings of California, Oregon and Washington. While the annual quota is likely to change as weak or strong year classes pass through the fishable stock, the long-term average is expected to be at about the 1991 level.

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shortbelly rockfish for surimi, but they have not submitted a permit request.



Shortbelly rockfish, *Sebastes jordani*.

SHORTBELLY ROCKFISH

History of the Fishery

The shortbelly rockfish (*Sebastes jordani*) is the most abundant rockfish off California but has been fished very little. A directed fishery occurred in 1982, when a joint venture with the USSR caught 700 tons off central California. Otherwise, a few shortbelly rockfish occasionally appear with other rockfish landed in California ports. There is no domestic market for shortbelly rockfish at present. If a market develops, special permits will be required, because fishing with legal mesh sizes is not practical for this small species. Large catches of shortbelly rockfish can be made using midwater or bottom trawls with fine mesh cod ends. Research has shown, however, that while directed fishing for shortbelly rockfish results in low incidental catches of other species when mid-water trawls are used, high incidental catches can occur when bottom trawls are used. Because of the concern that bottom trawls would take unacceptably high numbers of small fish of other important species, scientists have recommended against the use of bottom trawls for shortbelly rockfish.

The potential fishery for shortbelly rockfish is controversial. Fishermen express concern that significant amounts of salmon may be caught incidentally to fishing for shortbelly rockfish, but scientists have not observed incidental salmon catches and believe that a fishery for shortbelly rockfish is likely to be offshore from concentrations of salmon. Fishermen and environmental groups also express concern because young-of-the-year shortbelly rockfish are forage for salmon, sea birds and marine mammals. Scientists have recommended quotas that are thought to be sufficiently low so as not to impact either the recruitment or the availability of young-of-the-year shortbelly rockfish for forage. Scientists have also recommended close monitoring of fishing for shortbelly rockfish to verify that high incidental catches and/or depletion of forage do not occur.

The 1991 quota for catches off California, Oregon and Washington is 14,300 tons. Recent applications by joint venture companies to fish for shortbelly rockfish were not approved. These companies intended to use the catch for surimi. There has also been some interest expressed by domestic firms to utilize

Status of Biological Knowledge

Shortbelly rockfish are found from Punta Baja, Baja California, to La Perouse Bank, British Columbia. Peak abundances are between the Farallon Islands and Santa Cruz, and off the Channel Islands. Young-of-the-year shortbelly rockfish have been observed in the surf line, and adults have been reported as deep as 930 feet. The peak abundance of adults is over bottom depths of 400 to 700 feet. Adults commonly form very large schools over smooth bottom near the shelf break. Schools are often near or on the bottom during the day and tend to be less dense and higher in the water column during the night. The size of shortbelly rockfish tends to increase with bottom depth.

The maximum recorded age for shortbelly rockfish is 22 years, but fish older than 10 years are uncommon. Most are less than 11.5 inches in length, which corresponds to a weight of 0.5 pound. The maximum size is 12.8 inches, or about 0.7 pound. Early growth is fairly rapid, and by age three the average size is 7.8 inches for males and 8.3 inches for females. Growth has slowed by age eight, and the average size is 9.7 inches for males and 10.3 inches for females. About 50 percent of female shortbelly rockfish are mature by age three, and almost all are mature by age four. The fecundity ranges from 6,200 eggs for a 6.8-inch fish to 50,000 eggs for a 12.0-inch fish.

Plankton surveys during the January-April parturition season indicate that larvae are released in the same areas inhabited in the summer and fall by large aggregations of adults. However, the fish may be more dispersed during the late winter season because aggregations of adults have been difficult to locate then. The larvae are about 0.2 inch when released. The young fish lead a pelagic existence until June, when they are about five months old. In June, the young shortbelly rockfish begin to take on the behavior of adults. Divers occasionally observe them in large, compact, schools in fairly shallow water. Large numbers of moribund young-of-the-year shortbelly rockfish are sometimes found on beaches after periods of wind patterns that are thought to cause currents which carry them into shallow waters. These fish have not appeared to be either starved or diseased. They appear to be maladapted to contact with the abrasive bottom when in the nearshore environment.

During the latter part of the pelagic stage, the two to three-inch shortbelly rockfish feed mostly on copepods and small stages of euphausiids. Adults feed primarily on euphausiids, but also consume some copepods. Young-of-the-year shortbelly rockfish are important prey items for salmon and sea birds

during the latter part of the pelagic stage. They have also be found in the diet of lingcod and northern fur seals. Adult shortbelly rockfish are occasionally found in the diet of larger predators such as lingcod.

Status of Population

The population is at the unfished level. Biomass estimates have been attempted on four hydroacoustic surveys from Santa Cruz to the Farallon Islands. Large aggregations needed for the hydroacoustic technique were found only for two of the four surveys. The two biomass estimates were 168,000 tons and 325,000 tons. It was estimated that the biomass in this area could support annual catches of at least 14,800 tons without reducing the spawning stock below levels thought to be needed to maintain good recruitment.

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LONG-TERM STUDIES OF CAPTIVE LION-TAILED MACAQUES. LINDBURG, D.G. AND FORNEY, K.A.

Introduction

Lion-tailed macaques (*Macaca silenus*) derive from the rain forests of the Western Ghats in southwest India. Following on several years of census activity, the wild population is believed to number in excess of 2000 individuals, and one recent estimate places the number closer to 5000 (KARANTH, 1985). The species is considered by the IUCN and most other conservation entities to be endangered. The first in-depth study of a wild population was carried out during 1973-75 (GREEN and MINKOWSKI, 1977). Shortly thereafter several Indian primatologists, including Kurup, Ali, Johnson, and Karanth, collected census and ecological data. Most notable in terms of socio-ecological investigations are the five years of intensive study by KUMAR (1987), between 1978 and 1984.

In captivity the lion-tailed macaque has been nearly exclusively a resident of zoological gardens. Its rareness and attractive phenotype are factors that have contributed to its value as an exhibit animal. Recent estimates place the size of the captive population at 450-500 individuals (GLEDHILL, personal comm.). Scientific interest in the species has increased in recent years in connection with the development of conservation programs.

In this report we compare results from nearly a century of life in captivity to information that has recently become available from field investigations. Captive demographics are affected directly by such human practices as withholding of breeding opportunities or loss of individuals through exportation. In other, less obvious ways, the life history of lion-tails may be influenced by nutritional and environmental (e.g. climate) differences in the two locales and by health care impacts on such parameters as survivorship and longevity.

Although the incompleteness of records from the earlier decades of confinement and the relatively small sampling of individuals from both populations are limiting factors, there are compelling reasons for making such comparisons at this point in time. Over 90% of the lion-tails living in zoos today are captive born. Since it is difficult to imagine a circumstance under which additional wild-caught individuals would be brought into the captive sector, future generations must derive from the brood stock now in hand. Timeliness is also found in the fact that detailed management plans have been drawn up for the North American population and are in the formative stages for populations in Europe and Japan. It seems important to these plans to have in hand a knowledge of the potential impact of captivity on demographic and life history variables. Information of this kind will aid in assessing the state of the captive population and in guiding management decisions.

Methods

Only data drawn from the lion-tails born in North American zoos are used to estimate parameters for the captive population. Methods of data collection for this population are described in LINDBURG et al. (1989). For the life table, a broader data set is used, in that animals which were either shipped out of North America or who were brought in from zoos in other countries are included for the years they resided in North America. This table was generated using a program written by Jonathan Ballou of the National Zoological Park, Washington, DC. Information on wild populations is derived exclusively from KUMAR (1987). Where essential to the drawing of valid comparisons, our analysis has followed sampling procedures used in the field. For example, in calculating annual birth rates we have used data from a com-

parable 5 year period and have included only those infants surviving at the end of each 'census' year in order to approximate Kumar's annual census of wild troops.

History of the North American zoo population

Although earliest records are scant, lion-tails probably first appeared in captivity in European zoos well over a century ago (JONES, 1985). In North America the earliest verifiable record was the importation of a single individual by the Philadelphia Zoo in 1899 (GLEDHILL, 1987). From then until the onset of World War II, small numbers appeared in zoos in New York City, St. Louis, Chicago and San Diego. The heaviest period of import was during the 1950s and 1960s (Fig. 1A), when 54.7% of all wild caught animals were obtained. Imports declined rather suddenly after 1965, the last definite record being a trio imported in 1968.

Slightly smaller numbers of lion-tails of unknown origin appear in zoo records in roughly the same temporal pattern as shown by imports (Fig. 1B). It is reasonable to assume that the majority of these were also of wild provenance, particularly in the pre-war years.

The first captive births of record are three infants born at the Philadelphia Zoo between 1932-36. However, nearly three decades were to pass before births began to occur on a regular basis (Fig. 1C). Considering all sources, then, it can be seen (Table 1) that of nearly 600 lion-tails of record in North American zoos, 72% can be confirmed as captive born, with the vast majority of these occurring in the last two decades. On the basis of these data, the captive history of lion-tails can be divided into three periods:

1. 1899-1953 An initial period of over 50 years' duration in which the goal was to add lion-tails to exhibit collections exclusively through stock drawn from the wild.
2. 1954-1982 A transitional period, marked initially by frequent imports, but also a time when births would eventually exceed imports in annual additions to the captive stock.
3. 1983-present The final period, beginning with publication of a studbook, is indicative of an organized attempt among cooperating zoos to manage the captive gene pool in ways designed to preserve genetic diversity. This effort, like those for other endangered species, was in response to the precarious status of the wild population and to the realization that such steps would have to be taken to sustain the captive population (FOOSE and CONWAY, 1985).

Table 1: Origin of North American Lion-tailed macaques 1899-1986.

DECADE	SOURCE					
	Wild #	%	Unknown #	%	Captive born #	Total #
- 1909	8	100.0				8
1910 - 1919			2	100.0		2
1920 - 1929	9	75.0	3	25.0		12
1930 - 1939	17	70.8	4	16.7	3	24
1940 - 1949	4	80.0	1	20.0		5
1950 - 1959	39	57.4	11	16.2	18	68
1960 - 1969	29	23.2	30	24.0	66	125
1970 - 1979			10	5.9	160	170
1980 - 1986					175	175
Total	106	18.0	61	10.4	422	589

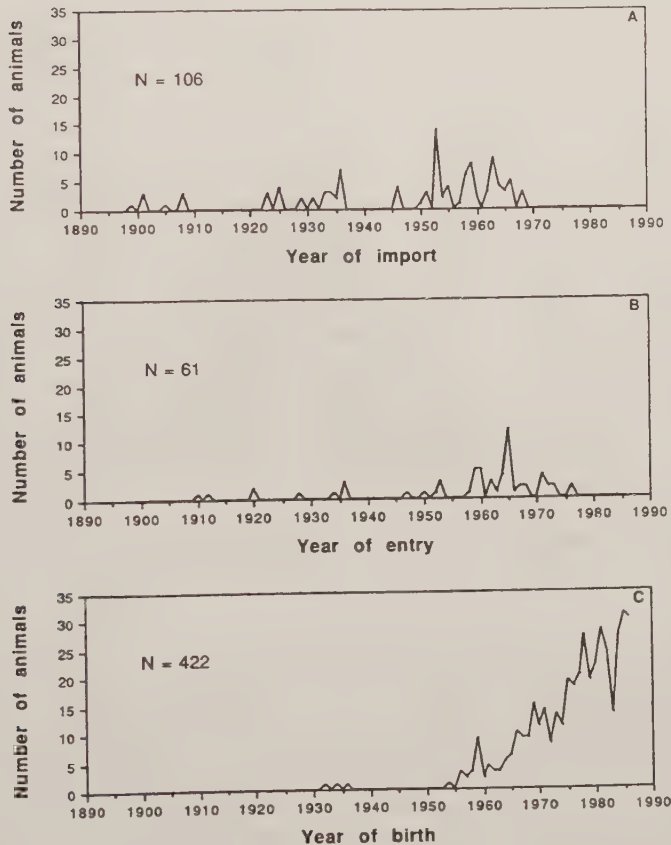


Fig. 1: Provenance of the captive North American population of lion-tailed macaques, 1899-1986. A = wild caught, B = unknown origin, C = captive born.

Population structure

The structure of the captive population at the end of 1986 is shown in Figure 2. The first 6 age classes are designated as immatures, following age criteria applied to the wild population, and comprise 52.3% of the total. In the wild, immatures averaged 47.3% of the population during 5 years of censusing.

Although the numbers for each sex in captivity are equal, this was achieved in part by shipment of 'surplus' males to zoos overseas, beginning in 1977. It has previously been reported that the captive sex ratio at birth strongly favored males (58.5%), and that males experienced a higher rate of mortality than females (LINDBURG et al., 1989). No data on natal sex ratios from wild lion-tails have as yet been reported. The most striking contrast between the wild and captive population is the proportion of adults (including subadults) of each sex. Whereas they occur in nearly equal numbers in the present-day captive population, comprising 22.9% and 24.8% respectively for males and females, males comprise only about 14% of the total in Kumar's study population. This compares with 39% adult and subadult females in the wild.

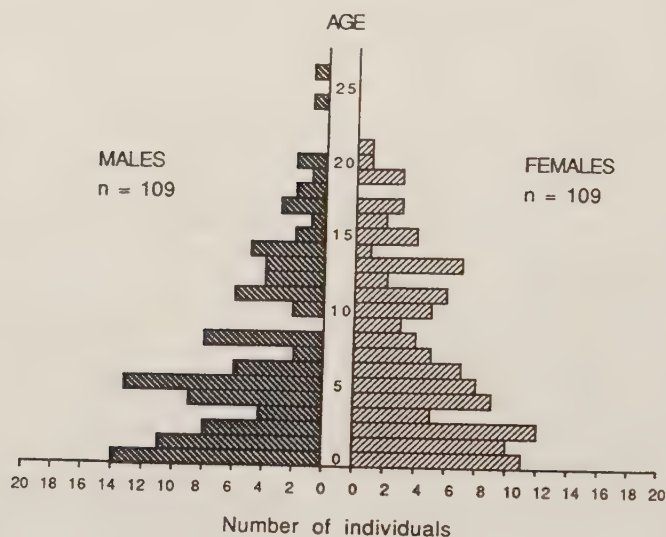


Fig. 2: Population pyramid for the captive population, 1986.

Birth rates

The birth rate is commonly defined as the number of offspring of either sex produced by breeding age females annually (ALTMANN and ALTMANN, 1970; DUNBAR, 1987). KUMAR's (1987) data on this point are based on an annual census of 3-6 troops, and results for 5 years indicate a mean rate of about 30% (Table 2). The interval between births in 3 observed cases averaged 29.7 months, but is probably an underestimate, given the number of infants seen during the study. The mean birth rate in the captive sector during an equivalent 5 year period was 29.5% (Table 2), whereas birth intervals for both lactating and non-lactating females combined (n=189) averaged 16 months.

Table 2: Comparison of Lion-tailed macaque birth rates in wild and captive populations

WILD		CAPTIVE	
1979 - 80	0.22	1982	0.31
1980 - 81	0.26	1983	0.17
1981 - 82	0.26	1984	0.32
1982 - 83	0.40	1985	0.34
1983 - 84	0.34	1986	0.32
5-year mean	0.299		0.295

Age-specific fertility (Mx) for captive lion-tails is presented numerically in the life table (Table 3) and plotted in Figure 3. Above age 18 the fertility rates were highly erratic, which, for females, is due to extremely small sample sizes (0-2) per age class. Although current study-book records list one female who first reproduced at 23 months of age (age class 1 in the life table), this is undoubtedly a reporting error. Excluding this case, the earliest birth of record in

the captive population was at 2.8 years, whereas mean age at first birth was 4.9 years (LINDBURG, et al., 1989).

Table 3: Lion-tailed macaque life table: Captive born North American population through 12/31/86

MALES				FEMALES			
AGE	Px	Lx	Mx	AGE	Px	Lx	Mx
0	0.739	1.000	0.000	0	0.819	1.000	0.000
1	0.933	0.739	0.000	1	0.966	0.819	0.005
2	0.956	0.689	0.000	2	0.944	0.791	0.005
3	0.961	0.659	0.016	3	0.978	0.747	0.086
4	0.957	0.633	0.128	4	0.964	0.730	0.186
5	0.962	0.606	0.239	5	0.958	0.704	0.343
6	0.985	0.583	0.252	6	0.984	0.675	0.290
7	0.967	0.574	0.337	7	0.964	0.664	0.385
8	0.961	0.555	0.253	8	0.979	0.640	0.263
9	0.956	0.534	0.384	9	0.976	0.626	0.291
10	0.977	0.510	0.330	10	0.974	0.611	0.371
11	1.000	0.499	0.314	11	1.000	0.595	0.465
12	0.969	0.499	0.321	12	0.965	0.595	0.300
13	0.962	0.483	0.383	13	1.000	0.575	0.447
14	0.949	0.465	0.229	14	0.947	0.575	0.392
15	1.000	0.441	0.408	15	1.000	0.544	0.459
16	1.000	0.441	0.415	16	1.000	0.544	0.323
17	0.753	0.441	0.526	17	1.000	0.544	0.391
18	1.000	0.332	0.532	18	0.875	0.544	0.580
19	1.000	0.332	1.235	19	0.810	0.476	0.127
20	1.000	0.332	0.672	20	1.000	0.386	0.417
21	1.000	0.332	1.653	21	1.000	0.386	0.615
22	1.000	0.332	1.929	22	1.000	0.386	1.115
23	1.000	0.332	1.102	23	0.968	0.386	0.000
24	1.000	0.332	0.964	24	1.000	0.373	0.000
25	1.000	0.332	2.204	25	1.000	0.373	0.000
26	1.000	0.332	1.136	26	1.000	0.373	0.000
27	1.000	0.332	0.000	27	1.000	0.373	0.000
28	0.000	0.332	0.000	28	0.000	0.373	0.000

Since adult ages could not be reliably estimated in the wild, no information on age-specific fertility for this population is available. However, KUMAR (1987) cautiously estimated the age at first reproduction for five young females followed over several years of observation as occurring at a mean age of 6.6 years.

For captive born males, average age at first reproduction has been reported as occurring at 6.6 years (LINDBURG, et al., 1989). Fertility rates beyond age 18 showed considerable fluctuation, as was noted earlier for females. Although the number of births per age class for these older males was slightly higher (2-10) than for females of equivalent age, the results are likely to be biased due to unequal breeding opportunities. Data on age at first reproduction for males in the wild state are as yet unavailable.

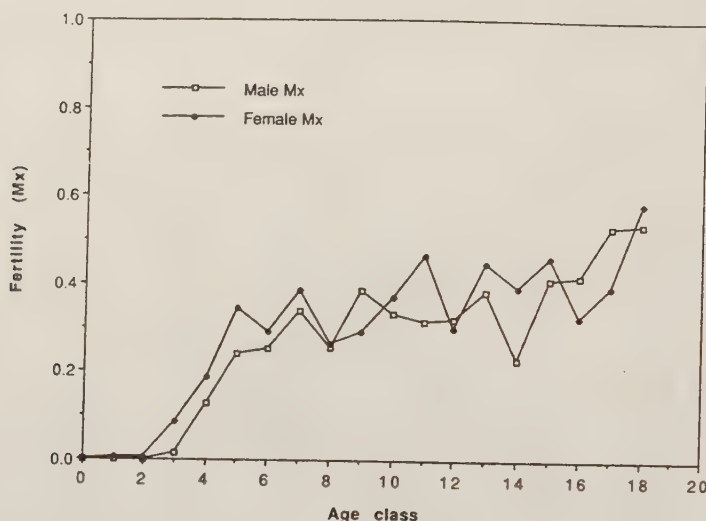


Fig. 3: Age-specific fertility of captive lion-tailed macaques.

Mortality

First year mortality of captive born lion-tails, based on our life table (Table 3) occurred at a rate of 26.1% for males and 19.1% for females. (See also Figure 4 for plotted estimates of age-specific survivorship for both sexes.) A life table by definition excludes unsexed individuals and therefore does not account for approximately 20 infants of unknown sex that were either stillborn or that died shortly after birth. Inclusion of these individuals brings the overall mortality rate during the first year of life to just over 28%, as reported by LINDBURG, et al. (1989).

To these results may be added the finding that captive mortality during the first year of life has declined from 48.6% of births during the early 1960s to 19.5% in the most recent three year period, 1984-86 (Figure 5). Also, captive living adults have shown a survival rate of 98.5% over the last five years of record (1982-86).

For wild troops KUMAR (1987) gave a mean survival rate of 96% for all age classes, drawn from a sample of 319 animal years. Though the exact numbers dying each year could not be distinguished from losses due to emigration, it seems quite certain that overall mortality rates in the wild were low. For example, in the immature age classes (up to 6 years of age) only 6 to 8 individuals disappeared from the 8 troops under surveillance during 6 years of census activity, despite the birth of 43 infants during this same period. The field data, unfortunately, do not permit a comparison of first year mortality rates to those in the captive sector.

Discussion

In the wild state lion-tailed macaques are described by KUMAR (1987) as having a late onset of reproduction, a low birth rate, and high survivorship during infant and adult stages. It is notable that Kumar's conclusions are in general agreement with those of GREEN and MIN-KOWSKI (1977), who initially characterized wild females as late to mature and as reproducing infrequently. In zoos, on the other hand, females begin reproducing earlier but lose offspring during infancy at a much higher rate than in the wild.

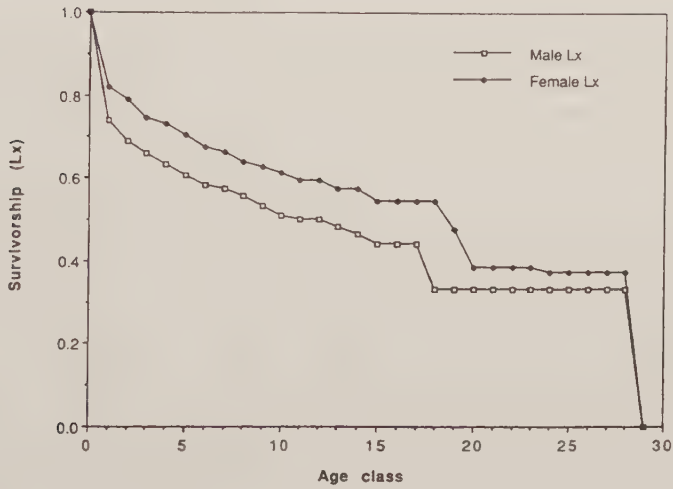


Fig. 4: Age-specific survivorship of captive lion-tailed macaques.

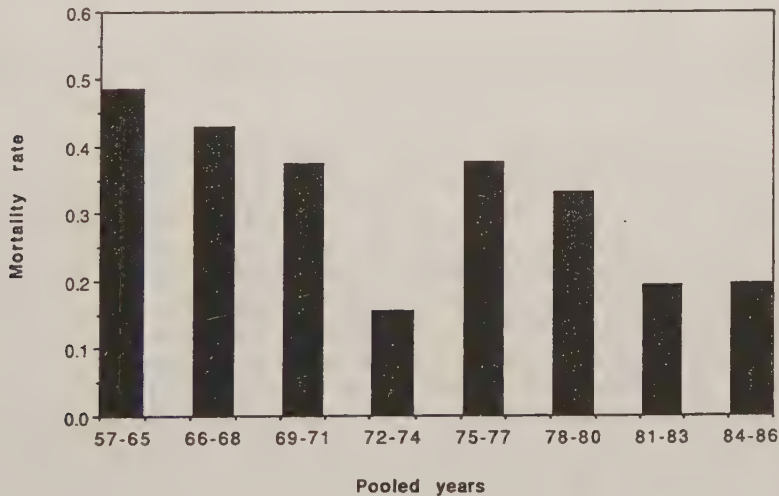


Fig. 5: First year mortality of captive-born lion-tails, 1957-1986.

An advancement in the age of first reproduction has been shown to occur in a number of wild primate populations that are provisioned (LYLES and DOBSON, 1988; LOY, 1988), suggesting a beneficial effect of nutrition on female maturation and reproduction. Since zoos are locales in which "the effects of resource limitation" are minimized (LYLES and DOBSON, 1988), it should not be surprising to find a similar result in our comparison of captive and wild lion-tail populations.

A shortened interval between births, perhaps by as much as 40 to 50%, may be a second effect of improved nutrition in the captive sector. As noted earlier, intervals in the wild are unusually long for macaques--provisionally placed at about 2.5 years but possibly averaging closer

to 3.5 years--and are undoubtedly a major reason for its low birth rate. Some of the interval difference is attributable to the different mortality rates for infants in the two populations, but even so intervals of captive females are much shorter than for the wild population when only females whose infants survived to one year of age are considered (LINDBURG et al., 1989).

In other respects the beneficial effects of provisioning, seen to occur in wild primates, are not so evident in the captive lion-tail population. Whereas one of the primary effects of enhanced food resources is to lower mortality rates (LYLES and DOBSON, 1988), even the first year mortality rate of 19% seen in recent years in zoos runs appreciably ahead of mortality rates in the wild. The decline in mortality of the zoo-based population from approximately 50 to 19% (shown in Figure 5) corresponds in time to an era of increased attention to captive breeding, and thus to related improvements in housing and management. This decline offers presumptive evidence of the impact of factors other than nutrition on survivorship in zoos.

An increased birth rate is yet another major effect to emerge from studies of provisioned populations (LYLES and DOBSON, 1988; Loy, 1988). Too little information is available from the wild population to permit valid comparisons of this parameter, but it should be pointed out that over a third of sexually mature females in captivity have not borne offspring (LINDBURG et al., 1989). The birth rate used here (see Table 2) includes 12 females aged 15 or beyond that had never reproduced, and which therefore contributed only zero scores to the 5 year period used for comparison to the wild population. We suspect that neglect of social, environmental, and health requirements have been the more likely causes of reproductive failure in these females. Relatively high female infertility rates may therefore be a major reason for the low captive birth rate and one of the major concerns deserving attention in managing the captive population.

From the foregoing we conclude that the close agreement in birth rates between wild and captive populations is attributable to different factors and is thus in part coincidental. But a real species difference might also be indicated by the fact that a birth rate of 30% for both captive and wild lion-tails is low compared to reports for other macaques, e.g., 49% for *M. sylvanus* (FA, 1986), 80% for Cayo Santiago rhesus (RAWLINS and KESSLER, 1986), and nearly 77% for unprotected rhesus in India (SOUTHWICK et al., 1980). In discussing this point, KUMAR (1987) notes that the birth rate in the wild is lower than would be predicted by allometry and may represent an adaptation of the species to rain forest habitat.

One of the more critical issues for the captive population is the proportion comprised of adult males. It is invariably the case that in wild macaque populations, adult females outnumber males by 2 or 3 to 1 (MELNICK and PEARL, 1987). With proportions of 14% and 39% respectively for males and females, wild lion-tails are no exception to this general finding. As yet no information exists on sex ratios at birth in the wild population, but since these ratios generally approach parity in large macaque breeding colonies (e.g. RAWLINS and KESSLER, 1986; PAUL and KUESTER, 1988) and in wild primates generally (DUNBAR, 1987), we may assume that the adult proportions in the wild are largely attributable to a higher mortality rate for males.

In captivity, also, males experience a higher mortality than females, but much of this difference is in the first year of life. Presumably, since infant mortality is quite low in wild troops, males in that locale continue to undergo heavier mortality after infancy. By contrast, harem grouping in captivity reduces the incidence of conflict among juvenile and reproductive age males, and probably therefore increases the survivorship of these age classes. This situation is further exacerbated by the strongly male-biased sex ratio at birth. Although the higher incidence of male offspring is unexplained, its occurrence in artificially maintained primate

populations has been shown by van SCHAIK and van NOORDWIJK (1983) to be common. These authors further suggest that social stress may lead females under these conditions to bias the sex of their offspring in favor of males. While resolution of this question must be left to future studies, it is clear that the male-biased natal sex ratio and relatively protected existence of males in the captive sector continue to produce a substantial population of singly housed males that are often referred to as the "surplus male" problem.

In summary, birth rates in both the captive and wild populations are low by comparison with other macaques and could be an indication of a species difference in reproductive capacity. However, the captive birth rate reflects the inclusion of a substantial number of infertile females, and represents an important focus for further research. Although females in the captive sector begin reproducing at an earlier age than their wild counterparts, the rate at which their infants perish suggests the need for more attention to disease, crowding effects, and socially induced trauma. From a captive management standpoint, one of the more burdensome aspects is the proportion of "surplus" adult males. The solution to this problem is complex, entailing the cost of maintaining unneeded individuals, the need to satisfy the genetic requirements of a small population, and the development of alternatives to housing this surplus in the limited space available in zoos.

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Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report

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ABSTRACT

Regimes of high abundance of sardine (*Sardinops sagax* and *Sardina pilchardus*) have alternated with regimes of high abundance of anchovy (*Engraulis* spp.) in each of the five regions of the world where these taxa co-occur and have been extensively fished. When one taxon has been plentiful, the other has usually been at a reduced level of abundance, and vice versa. Changes in the four heavily fished regions that support *S. sagax*—the Japanese, Californian, Humboldt, and Benguela systems—from a regime dominated by one taxon to a high level of abundance of the other have occurred more or less simultaneously. In the Pacific Ocean, sardines have tended to increase during periods of increasing global air and sea temperatures and anchovies to decrease. The Japanese system is dominated by sardines to a greater extent than the other systems, and sardines off Japan appear to increase as the Kuroshio Current cools. At the eastern edge of the Pacific Ocean, sardines colonize cooler areas during periods of warming. The Benguela system is out of phase with the three Pacific systems. The four systems all appeared to be in a state of flux in the 1980s. Increased abundance of the

subdominant taxon is often one of the first signs of change. Sardines are relatively sedentary in refuge areas when scarce but change behavior to become highly migratory and colonize cooler areas when abundant. Anchovies, by contrast, expand around a fixed geographic center.

Key words: sardine, anchovy, global temperature change, abundance, regime changes, Kuroshio Current, California Current, Humboldt Current, Benguela Current

INTRODUCTION

Sardines are extensively fished in five of the world's coastal regions, off Japan and in the California, Humboldt, Benguela, and Canary current systems, but only slightly off Australasia. Sardines in five of these six regions are believed to be the same species—*Sardinops sagax* (Parrish et al., 1989). The sardine of the Canary Current system, including the Mediterranean and the North Sea, is a distinct genus—*Sardina pilchardus*. Anchovies (*Engraulis* spp.) have a wider distribution than sardines but co-occur with sardines in each of the six regions.

Populations of sardines and anchovies or both have undergone large changes in abundance in each of the five regions where they co-occur and have been extensively fished (Lluch-Belda et al. 1989). Often, anchovies were abundant when sardines were relatively scarce and vice versa (e.g., Daan, 1980; Silvert and Crawford, 1988). Sardines in the different regions of the Pacific Ocean and in the Canary Current tend to be abundant at almost the same time (Kawasaki, 1983, 1991b; Lluch-Belda et al., 1989). Catches of sardines in the Benguela Current are high when they are low elsewhere and vice versa (Crawford et al., 1991), thus being out of phase with the other locations. There is accumulating evidence that in all four regions where there are large fisheries for *S. sagax*, changes in the relative abundance of sardines and anchovies were initiated in the second half of the 1980s.

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From a 1988 workshop in La Paz, Baja California Sur, Mexico, these synchronous massive changes in abundance were described as a "regime problem" with global manifestations (Lluch-Belda et al., 1989). In November 1990 the authors again held a workshop in La Paz to discuss the large fluctuations that have taken place in the populations of sardines and anchovies. This paper documents the conclusions of that workshop, including the general characteristics of the regime cycle, as well as the recent variations in areas of major *S. sagax* fisheries.

THE REGIME CYCLES

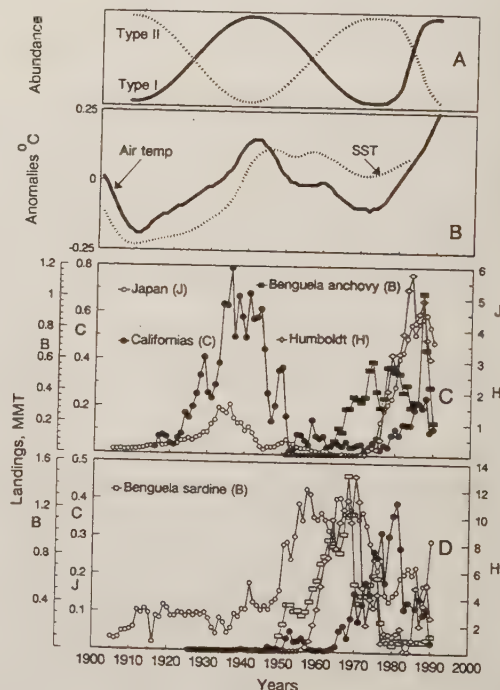
Based on the definition given by Lluch-Belda et al. (1989), the two phases (high and low) of the regimes of abundance of sardine and anchovy fishing were analyzed for each of the major areas using the existing historical data as well as personal experience. Catch data show that the sardine populations off Japan and California were in the high-abundance phase during the 1930s. These data also show the high-abundance phase during the 1980s off Japan, California, and Chile-Peru (Fig. 1C) as well as pilchard in the Canary Current. The low-abundance phase was present off Japan and California in the early 1900s, and from the 1960s to the early 1970s it was present off Japan, California, the Humboldt Current (Fig. 1C), and the Canary Current. The reverse was true for anchovies off Japan and California, in the Humboldt Current, and in the Benguela Current; sardines were abundant in 1960s and early 1970s but subsequently scarce, whereas anchovies showed the opposite trend (Fig. 1C, 1D).

The regime cycles are of two types. Type I includes sardines, while anchovies belong to type II. Each of the types has its particular ecological characteristics and strategies. Sardines in the Benguela Current belong to type I, notwithstanding that their cycle is out of phase with the other sardine populations. Except for the Benguela sardine the high-abundance phase of the type I is associated with global warm periods, while the contrary is true for the high-abundance phase of the type II. In other words, sardines tend to be abundant during high-temperature global regimes, while anchovies are abundant during low-temperature global regimes. This is illustrated in Fig. 1 for the full series available and in Fig. 2 for the expanded 1960–1990 period.

BIOLOGICAL CHARACTERISTICS OF THE TWO REGIME TYPES

There are significant differences between the two regime types. Sardines expand and contract their geo-

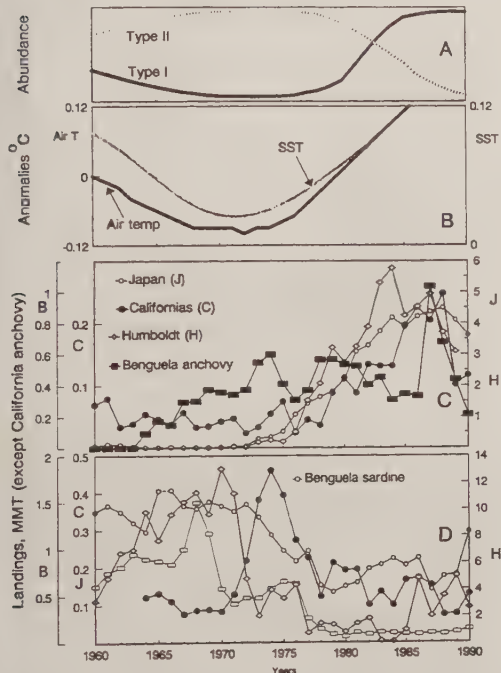
Figure 1. (A) Schematic cycles in regimes of abundance of sardine and anchovy. (B) Global air and sea surface temperatures anomalies as digitized from Jones (1991) and Reid (1987, 1991), detrended by means of q-spline procedure in a commercial statistical software package to remove the high-frequency variation. (C) Japanese (J), California–Baja California west coast–Gulf of California (C), and Humboldt (H) sardine landings and Benguela (B) anchovy landings. (D) Japanese (J), California (C), and Humboldt (H) anchovy landings and Benguela (B) sardine landings.



graphical range much more than anchovies do. Sardine populations expand rapidly poleward during warming periods, greatly shifting their main spawning and feeding areas. Anchovies seem to expand and contract around a fixed geographical center (Lluch-Belda et al., 1989).

Type I species, notably sardine, exhibit the phenotypic changes that correspond to the Kawasaki migratory phenotypic forms (Kawasaki, 1983). This biological variation, called phase variation, is similar to that long recognized in locusts, in which there are both solitary and gregarious phases. For example, the Far Eastern sardines, in the high-abundance phase, acquire smaller body sizes at the same ages and the capability of swimming longer distances as they occupy new,

Figure 2. Expanded plots from Fig. 1 during the period of 1960–1990, except that the California anchovy series is estimated biomasses instead of landings, since catches were initiated later.



broader, more productive areas. In the low-abundance phase, however, they are more or less restricted to limited areas, larger in body size at the same age, and non-migratory.

Type II species do not show these phenotypic shifts. Their populations seem to be distributed more evenly along their normal geographical range. When the type I species decline in numbers or are at low levels, the type II species have the ability to increase rapidly to very high numbers within their normal geographic range.

Genetic homogeneity might be expected in the type I species, owing to their being restricted to small refuge areas during their low-abundance phase where genetic interchange is higher. Since type II species do not contract or expand their geographic range significantly, they might be expected to have genetic heterogeneity. Hedgecock (1991) showed this to be the case for the California sardine and anchovy. Thus, both types of species are utilizing the high-productivity upwelling areas with quite different ecological genetic strategies.

RECENT CHANGES IN FOUR CURRENT SYSTEMS

The Japanese system

Twice this century, sardines have been abundant in waters around Japan. Large catches were made from the late 1920s to the mid-1940s. They were scarce through the 1950s and 1960s, but there was a spectacular increase in abundance starting in 1975 (Kondo, 1980). The highest ever annual catches were recorded in the late 1980s, when harvests were about 4.5 million tons (Fig. 1C). Landings of anchovy were low during the 1930s and 1940s, greatly increased in the 1950s and 1960s, and then decreased in the 1970s. However, during the 1980s, catches of anchovy increased to slightly above the level of the 1940s (Lluch-Belda et al., 1989), and in 1990 the increase in catch was from 182 thousand tons to 296 thousand tons (Fig. 1D).

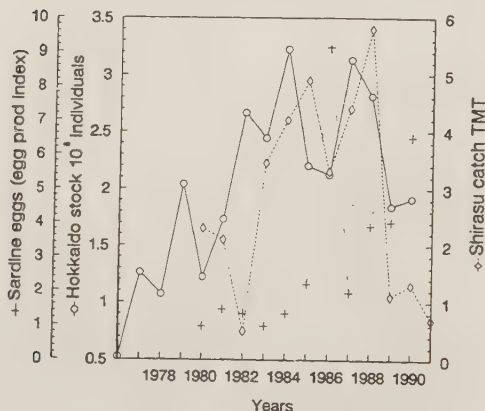
Although high catches of sardine were maintained until 1988, the abundance of sardine around Japan is believed to be decreasing. Available stock indices and catch rates have fallen in the northern fishing grounds off eastern Hokkaido (Fig. 2) (Wada and Kashiwai, 1991), a region where sardine is usually scarce during periods of low abundance (Lluch-Belda et al. 1989, Parrish et al. 1989). Further, there has been a recent increase in the growth rate of sardines. In the past there has been a density-dependent increase in growth rate at low stock sizes (Wada and Kashiwai, 1991). Another possible indication of a decreasing sardine biomass is the commercial catch of shirasu, larval sardine that is a highly prized delicacy in Japan. The catch fell markedly in 1989, continued to be low in 1990 without any decrease in fishing effort (Wada and Kashiwai, 1991), and fell further in 1991 (Fig. 3). The reduced shirasu catch occurred in spite of an abundant production of sardine eggs, as shown in Fig. 3 (Mori et al., 1988; Kikuchi and Konishi, 1990), indicating high mortality of ichthyoplankton.

By contrast, research boats have recently encountered exceptionally large shoals of anchovy, suggesting that the abundance of this species may be increasing. Anchovy catches began increasing in the 1980s (Fig. 1D).

The California Current

Sardines were abundant in the northern portion of the California Current in the 1930s with catches exceeding 0.7 million metric tons (MMT) per year (Murphy, 1966), but the population declined by several orders of magnitude during the 1940s and 1950s and remained at very low levels until the late 1980s (Smith, 1990). From the mid-1970s, substantial catches of sardine were made in the Mexican fishery off central and

Figure 3. Sardine abundance indices off Japan.



southern Baja California but primarily in the Gulf of California (Fig. 4) (Lluch-Belda et al., 1989). Anchovy abundance increased markedly during the late 1960s to a peak in the mid-1970s and remained at high levels through the mid-1980s (personal communication). Anchovy catches peaked at over 0.3 MMT in 1981 but have declined to an average of about 0.1 MMT from 1983 through 1989 and fell to about 0.03 MMT in 1990 (Fig. 1D).

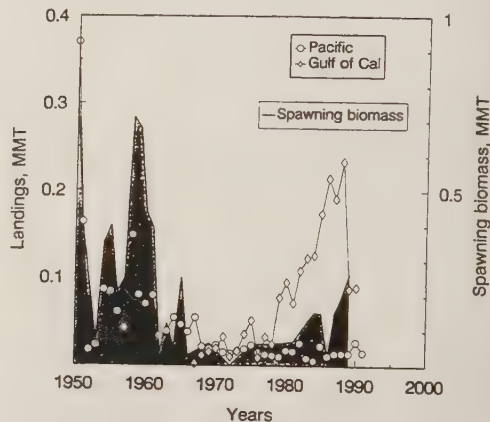
The sardine spawning biomass, which had been at extremely low levels for several decades, increased sharply during the 1980s (Fig. 4) (Smith, 1990). The estimate for the California sardine biomass for 1990 is between 100,000 and 600,000 tons (Barnes et al., 1991). This does not include the biomass off Baja California or the Gulf of California.

The Gulf of California may be a special location. The sardine fishery began in the late 1960s (Lluch-Belda et al., 1986). The catch increased over the years until 1988 and then dropped dramatically starting in 1989 (Fig. 4). The anchovy (*Engraulis mordax*) was first caught in the Gulf of California in 1986 (Hamann and Cisneros-Mata, 1989). Before that time, no eggs, larvae, or adults were ever recorded as having been in the Gulf. Anchovy currently dominates the fishery.

The Humboldt Current

Purse-seine fisheries off Peru and Chile developed after the sardine collapse in California in the late 1950s, with catches initially being dominated by anchovy. The anchovy fishery collapsed in the mid-1970s; landings plummeting from in excess of 13 MMT to less

Figure 4. Sardine spawning biomass off California and landings of the Pacific coast and Gulf of California.

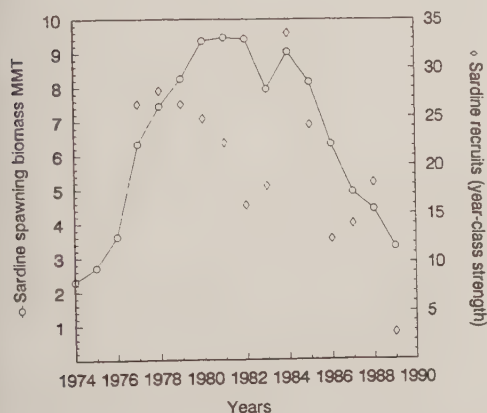


than 1 MMT in the space of a few years. Landings remained at low levels for a period of about 10 years, fluctuating between about 50 thousand and 4 million metric tons. Landings of sardine rose from about 20 thousand tons in the 1960s to more than 5 MMT in the mid-1980s. The catch has subsequently decreased, principally owing to the rather rapid decline of the Chilean catch.

Different stock units exist along the margin of the southeast Pacific (Serra, 1983; Parrish et al., 1989). The sardine and anchovy stocks off northern-central Peru and southern Peru–northern Chile are the largest and are those that sustain the main pelagic fisheries in the two countries (Serra, 1983; Zuta et al., 1983; Serra and Tsukayama, 1988). The fisheries in Peru and Chile are managed independently.

Off Chile, there was a sustained decrease in the biomass of sardine aged three or older throughout the 1980s (Serra, 1991; personal communication). The biomass at the end of the decade was only about 40% of its level in 1980 (Fig. 5). Virtual population analysis suggests that weak year-classes were formed in 1982 and 1983, coinciding with the El Niño event of 1982–1983 (Fig. 5). These year-classes begin entering the exploitable population during 1986 and 1987 as fish aged three. Subsequent year-classes show a slight recovery but then a marked decrease in 1986, indicating that the resource is entering a phase of lower abundance. The start of the Chilean sardine decline has been blamed on overfishing (Serra, 1991; personal communication). However, the weak year-classes since 1986 began with entry to the spawning stock of

Figure 5. Sardine spawning biomass and recruits in the southern Humboldt Current.



the poor year-classes formed during the 1982–1983 El Niño.

Catches of anchovy off Chile and Peru have increased since the mid-1980s, and almost 5 MMT were landed in 1989 (Fig. 1D). After the 1982–1983 El Niño, intensive spawning of anchovy was recorded off northern Chile (personal communications). There was also a shift in the species composition of ichthyoplankton back to that typical of the late 1960s, when anchovy was dominant (Loeb and Rojas, 1988). Off northern Chile, virtual population analysis suggests that a powerful year-class of anchovy was formed in 1987, and this led to a biomass of spawners (fish aged one or older) in 1988 and 1989, more than double the level of 1984 (personal communication).

The Benguela Current

In the Benguela Current, sardine dominated purse-seine catches in the 1950s and 1960s, but it was replaced in the catches by anchovy in the 1970s (Crawford et al., 1987). Anchovy continued to dominate catches in the early 1980s, and a peak of nearly 1 MMT was landed in 1987. Thereafter, there was a rapid decrease in landings (Fig. 1C).

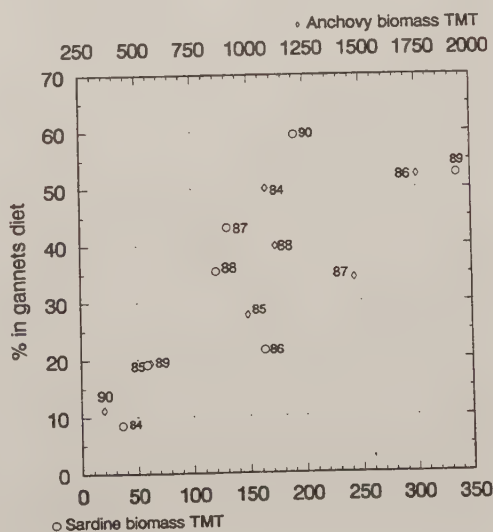
Stocks of sardine and anchovy off Namibia and South Africa are believed to be relatively discrete (Crawford et al., 1989) and are managed independently. Since the mid-1980s the biomass of anchovy spawners off South Africa has been measured by acoustic surveys (Hampton, 1987). Estimates of biomass were at first considerably higher than those calculated by virtual population analysis (e.g., Newman and

Crawford, 1980). The total allowable catch was approximately doubled in 1987 and 1988, and this was the main reason for the exceptionally high catches from the Benguela Current in these years.

Since the late 1970s the diet of Cape gannets (*Morus capensis*) has been monitored at two of its breeding localities off western South Africa on a monthly basis (Crawford and Shelton, 1981; Berruti, 1987). The annual contribution, by mass, of sardine and anchovy to the diet of Cape gannets reflects the changes in the biomass of the two prey species as measured by acoustic surveys (Fig. 6). In the 1980s there was a decrease in the contribution of anchovy to the diet of Cape gannets, with 1989 and 1990 being the lowest levels recorded to date and confirming low acoustic estimates of abundance of anchovy in these years. By contrast, the contribution of sardine to the diet of Cape gannets increased steadily after 1984, and in 1990 sardine contributed about 60% of the diet (Fig. 6).

It appears that sardine may currently be replacing anchovy as the dominant small planktivorous fish in the southern Benguela Current. Landings of anchovy by the Namibian purse-seine fishery have been low since 1984, except in 1987 when, as off South Africa, there was a large catch. Landings of sardine off Namibia increased through the decade by almost an order of magnitude. This suggests that there may also be a shift

Figure 6. The relationship between sardine and anchovy biomass and contribution by mass of these species to the diet of Cape gannets.



in dominance in the northern Benguela Current from anchovy to sardine.

GLOBAL PHASE CHANGE

In each of the four systems where *S. sagax* is extensively fished, there is evidence for an increase in abundance of the low-abundance phase species since the mid-1980s. Catches of anchovy increased off Japan in the latter part of the decade, and research surveys also encountered increased quantities of anchovy. In the Humboldt Current, catches of anchovy increased in 1986 and have remained high since, although they show rather strong fluctuations. Off northern Chile a large anchovy year-class was formed in 1987, and it caused a large increase in spawner biomass in 1988 and 1989 (personal communication).

Off northern Baja California and southern California, where anchovy was the dominant species in the early 1980s (Lo and Methot, 1989; Smith, 1990), there is evidence that sardine increased toward the end of the decade. In the Benguela Current, where anchovies predominated in the 1970s and 1980, sardine has increased since 1984.

In most instances the high-abundance-phase species has decreased in abundance, but awareness of the decreases has arisen at various stages. The earliest suggestion that the abundance of sardine might be decreasing off Japan was a contraction in the eastward extent of the species range. In 1984, sardine was encountered across the northern Pacific to 174°W, but in 1985 and 1986 it was found only as far east as 174°E (Wada and Kashiwai, 1991). In the Gulf of California, sardine catches decreased substantially in 1989 and 1990. In the Humboldt Current, sardine catches decreased after 1985, but there was a clear trend to a reduced spawner biomass after 1982. Off California and northern Baja California, there was no indication of a decrease in anchovy, the dominant species, up until 1988. In the other region where anchovy dominated, the Benguela Current, the first indication of collapse was of an exceptionally poor year-class off South Africa in 1989. This was reflected in a sustained low contribution by anchovy to the diet of Cape gannets from mid-1989 onward.

Statistically significant relationships between historical records of catches off Japan, California, and South America suggest that changes in the Pacific Ocean occur simultaneously or with a short lag, depending on assumptions made concerning the age of recruitment of sardines to the fisheries (Crawford et al., 1991). Until the most recent changes, sardines in these three systems were in phase with one exception

(Kawasaki, 1983, 1991a; Kawasaki and Omori, 1988). Sardines off Japan, in the Humboldt Current, and in the Gulf of California attained high levels of abundance in the 1970s and 1980s, but sardines continued to be scarce off California and northern Baja California. At the time of the upswing in sardine abundance off Japan and in the Humboldt Current in the early 1970s, the biomass of sardine off California approached a zero level (Smith, 1990), but over the years the California sardine biomass has increased to between 100,000 and 600,000 tons (Barnes et al., 1991).

GEOGRAPHIC CHARACTERISTICS OF CHANGE

When sardine is replacing anchovy, as appears to have happened in the Benguela Current, the first signs of change may be an increased abundance of sardine. A reduced abundance of anchovy may be apparent only at a later stage.

When anchovy is replacing sardine, a contraction in the range of sardine, as off Japan and Chile, may be an early indication of change. Increased catches of anchovy were recorded off Japan, in the Gulf of California, and in the Humboldt Current from the mid-1980s, so in each instance considered, one of the first signs of change appears to have been an increased abundance of the subdominant species.

Altered behavior by *S. sagax* during periods of high and low abundance is of particular interest in that it is akin to the phase variation in such insects as locusts and armyworms (Dröschner, 1980). When at a low level of abundance, the species remains in coastal waters with a greatly reduced level of migration. At high abundance it becomes a widely migrating oceanic species, except when thermal barriers, for example, at the southern ends of Baja California west coast and the Gulf of California, restrict such behavior. We describe below the range expansions in each of the four systems we have considered.

Off Japan, at low abundance the sardine is restricted to the southern coasts of Honshu and Shikoku islands, with small pockets of spawning off these two islands. At high levels of abundance there is a large increase in range. Adult fish occur well into the oceanic Pacific, and they migrate northward along the eastern coast of Japan from July to October. This migration supports a large summer fishery off Hokkaido. Fish range even farther into the oceanic Pacific, where they were found east to 174°W in 1984 (Wada and Kashiwai, 1991). The species also colonizes the sea of Japan, where it is caught in coastal regions off western Japan and along the seaboard of the former Soviet Union and Korea

(Kawasaki and Omori, 1988). Spawning spreads to the north along the Pacific coast of Honshu and into the Japan Sea. When abundance is high, a large amount of spawning takes place off southern Kyushu Island.

Off California and northern Baja California, during periods of low abundance the sardine was still plentiful off central and southern Baja California. It retreated to its area of refuge (Lluch et al., 1991). Off California, from the early 1970s, when the sardine biomass was at a near-zero level, through 1990, it has expanded to between 100,000 and 600,000 tons (Barnes et al., 1991). At this time we cannot tell what is happening to the population biomass. The California sardine catch is not an index of abundance because of the state's imposed catch limits, and the cruises for estimating the biomass are not extensive. The catch in 1990 of pure loads of sardines was lower by about 12 percent from the year before off northern California (California Department of Fish and Game, 1991), perhaps a sign of reduced migration from the south.

In the Humboldt Current, sardines, when at a low level of abundance, spawn off northern Peru and off northern Chile. The main center of fishing is off northern Chile, and sardines are distributed from northern Peru to about 30°S. When sardines are abundant, spawning spreads along central Peru and also occurs at about 30°S and 36°S. The distribution extends north to Ecuador and south to about 40°S. Fishing takes place off southern Ecuador, northern and southern Peru, and northern Chile and at various localities off central Chile. The Chilean fishery is based on fish aged about three or older (Serra, 1983). It is not known whether the large southward extension in distribution is mainly attributable to these older fish, analogous to the northward migration of older sardine to British Columbia in the California Current (Murphy 1966), or whether a substantial number of juveniles also occur in the south. A limited number of juveniles have been caught in the south by research surveys. It is clear that the sardine fishery at Talcahuano (36°40'S) was declining while catches at Arica (18°30'S) were still at a high level. This is similar to the collapse of the Californian fishery for sardine from north to south in the 1940s and 1950s. The reduced catch started in British Columbia (50°N) and progressed southward to southern California (30°N) (Murphy, 1966; Radovich, 1982).

In the Benguela Current, at low levels of abundance, spawning by sardines is largely confined to northern Namibia (Le Clus, 1990) and to the western Agulhas Bank off South Africa (Crawford, 1991). Sardines are distributed off northern Namibia and southern South Africa but are scarce in intermediate areas

(Crawford, 1991). At high levels of abundance, spawning extends up western South Africa to Cape Columbine (Crawford, 1991), and sardines are often plentiful in the relatively cool water of the central Benguela system. For about a decade the sardines supported a fishery at Luderitz, the coldest portion of the Benguela Current with sea surface temperatures of 13°–14°C (Parrish et al., 1989). This fishery collapsed ahead of the fishery at Walvis Bay, similar to the early collapses of the cold-water fisheries off British Columbia.

There are several differences between the Japanese region and the other regions where types I and II prevail. The anchovy biomass has not reached anywhere near that of the sardine off Japan, unlike the other systems. Another difference is that the Kuroshio Current was cool during the 1980s at the peak of the sardine biomass and during the global warming phase. These differences may be a significant key to understanding the general phenomenon of regime shift. If regime shifts are associated with the strength of the major ocean gyres, a reduction in gyral flow would cause the eastern boundary currents to warm up (owing to less subpolar input) and cause the western boundary currents to cool off (owing to less tropical input). The lack of a large anchovy biomass off Japan may be due to the fact that cooling here produces more sardines, whereas cooling produces more anchovies in the eastern boundary currents.

Collapses of sardines in the Pacific Ocean have occurred at the same time that there has been a shift from warmer to cooler global temperature regimes; the reverse (the increased abundance of these populations) has been parallel to the shift of cool to warm global temperature regimes. Global temperatures, of both air and sea, appear to coincide with the regime events taking place in the sardine and anchovy populations, but the cause in each region may be a manifestation of some other event associated with the global temperature changes. As yet, we have not been able to determine what triggers the changes in each location.

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The daily fecundity reduction method: a new procedure for estimating adult fish biomass

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A new method was developed for estimating adult fish biomass from the daily decline in reproductive potential of the population and the numbers of planktonic eggs. Decline in reproductive potential was estimated from the product of the daily decline in the standing stock of advanced oocytes in ovaries and the daily decline in the numbers of females with reproductively active ovaries. Daily production of planktonic eggs was estimated from the number of eggs in quantitative oblique plankton tows. The method is restricted to fishes in which the potential annual fecundity becomes fixed prior to the onset of the spawning season, that is, fishes with determinate annual fecundity. The method was applied to data for *Microstomus pacificus*, commonly known as Dover sole, a pleuronectid flatfish of the upper continental shelf (200–1500 m) of the west coast of North America.

Key words: Biomass, eggs, ichthyoplankton, fecundity, *microstomus pacificus*.

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Introduction

The annual egg production method (Saville, 1964) has been widely used for estimating the biomass of adult fish from the numbers of planktonic eggs. Parker (1980) showed how a daily egg production method could also be used to estimate adult fish biomass. Subsequently, the daily egg production method has been used to estimate the biomass of sardines and anchovies (Santander *et al.*, 1984; Lasker, 1985; Wolf and Smith, 1986).

The principal difference between the daily and annual methods is in the way fecundity is estimated. In the annual method, one measures the standing stock of advanced yolke oocytes in the ovaries of females taken prior to spawning season. This estimate of fecundity is considered to be equivalent to the potential annual fecundity of the stock. This condition is called determinate annual fecundity (Hunter *et al.*, 1985; Horwood and Greer Walker, 1990), because the annual fecundity is assumed to be fixed prior to the onset of spawning. In contrast, the daily method uses daily fecundity which is the product of spawning frequency and the number of eggs released per spawning (batch fecundity). The daily method may be preferable because less cruise time is required but may be

costly because estimation of spawning frequency of the population requires either laboratory calibration or a series of samples of the spawners taken over 24 hours at sea. In addition, it may be more difficult to obtain representative samples of the adult population during the spawning season than before it begins. Thus, adult sampling from research vessels may be required for the daily method while for the annual method samples drawn from the commercial fishery may suffice.

The objective of this paper is to describe the daily fecundity reduction method (DFRM), a new method for estimating adult fish biomass from the numbers of planktonic eggs. This method is a daily method designed for fish of determinate annual fecundity and involves measuring the daily decline in the standing stock of advanced yolke oocytes (total fecundity) and the daily decline in numbers of females with reproductively active ovaries during a part of the spawning season. Fish biomass is estimated by linking the decline in the two reproductive variables (fecundity and ovarian activity) to the production of planktonic eggs. The chief advantage of the DFRM is that estimates of spawning frequency are not required. The DFRM is inappropriate for fishes with indeterminate annual fecundity, such as anchovy and sardine (Hunter

et al., 1985), because a key assumption underlying the model is that no new advanced oocytes are recruited to the ovary during the survey period. It may also be inappropriate to apply the DFRM to fishes having extensive spawning migrations since the DFRM requires representative samples of both spawning and spent females during the spawning season.

Material and methods

The general form of the model for the DFRM is:

$$B = \frac{P_o \times A}{(R/W) \times D_t \times 10^6} = \frac{P_o \times A}{K} \quad (1)$$

with approximate coefficient of variation (CV) of estimate of biomass

$$CV(B) = [CV^2(P_o) + CV^2(K) - 2COV(P_o, K)/(P_o K)]^{0.5} \quad (2)$$

where B is the biomass (mt) for area A .

P_o is the daily production of eggs per 10 m^2 sea surface area estimated from egg abundance adjusted for their development time and mortality during incubation.

A is the area size in 10 m^2 of the survey area. The quantity $K = (R/W) \times D_t \times 10^6$ in the denominator of equation (1) is daily population fecundity in units of eggs $\text{mt}^{-1} \text{day}^{-1}$, where R is the female fraction of the population by weight, W is the average female weight (g), D_t is the daily fecundity per female at Julian day t and is expressed as:

$$D_t = d(E \times G)/dt = E_t dG/dt + G_t dE/dt.$$

The quantity 10^6 converts grams to metric tons, E is the number of advanced yolked oocytes present in the ovary (total fecundity), G is the fraction of females that have ovaries containing advanced yolked oocytes (fraction of females with active ovaries), t is the elapsed time in days over which changes in G and E are monitored.

In the proposed model we use the two variables, G (fraction of females with active ovaries) and E (total fecundity) to measure the seasonal decline in the total fecundity of the population. G is measured on-ship using gross anatomical criteria to distinguish active (advanced yolked oocytes present) from inactive ovaries (no advanced oocytes present) and E is measured in the laboratory using conventional gravimetric fecundity methods. The decline in total fecundity (E) over time measures the rate the standing stock of advanced oocytes declines as batches are spawned; females that have completely exhausted their stock of advanced oocytes are not included in this measurement. The decline in G over time estimates the rate females pass from a reproductively active to an inactive state, i.e. the rate at which females

spawn all of their advanced oocytes. Thus the product of the rates of change in G and E measures the daily decline in fecundity of the average female in the population (D). In short, the decline rate of $E \times G$, $d(E \times G)/dt$ measures the daily decline in fecundity in the average female. The daily decline in the average female fecundity is converted to the daily decline in the fecundity of the population (K) using the ratio R/W , where R is the weight of female Dover sole (regardless of the level of ovarian activity) divided by the weight of male, female and immature fish of undetermined sex, and W is the average female weight in the sample. Both R and W are estimated for random samples of the trawl catch.

We assume that during a survey ovaries of the females in the population only change from active to inactive states, and not the reverse. Thus the survey must begin after the ovaries of most of the mature females in the population have developed sufficiently to be classified as active. Since any female taken in a trawl can be included in the denominator of G (the fraction of females with active ovaries), it follows that the biomass (B) is an estimate of the total adult biomass vulnerable to our trawl which includes all adult fish and an unknown fraction of the juveniles. This differs from the daily egg production method used for anchovy (Lasker, 1985), where spawning biomass rather than total "trawlable" biomass was estimated.

As in past methods, the daily production of eggs (P_o) is estimated from their abundance adjusted for egg development rates and natural mortality (Sette, 1943; Saville, 1964; Hewitt, 1985). This requires identification and staging of eggs and knowledge of temperature-specific rates of egg development.

Both direct formulas and resampling methods (jack-knife and bootstrap methods) were used to compute estimates of parameters, and their variances. Resampling methods were used primarily for estimation of the variance of biomass, covariances of adult parameter estimates and the bias of parameter estimates (Efron, 1982; Lo *et al.*, in press).

The example

Data sources

To illustrate the method, we used data for *Microstomus pacificus*, a pleuronectid flatfish commonly known as the Dover sole on the west coast of North America (Eschmeyer *et al.*, 1983). Dover sole are an appropriate example because: they do not have extensive spawning migrations (Quirollo and Kalvass, 1987); their potential annual fecundity becomes fixed before spawning begins, that is fecundity is determinate; and they do not spawn all their advanced oocytes at once but spawn about nine batches before using up their stock of advanced oocytes

(Hunter *et al.*, in press). Hunter *et al.* conclude that determinate fecundity is indicated by four lines of evidence: (1) in mature ovaries a hiatus exists between the advanced stock of mature oocytes and smaller, less mature oocytes; (2) total fecundity declines over the spawning season; (3) total fecundity is lower in females with post-ovulatory follicles; and (4) the mean diameter of the advanced oocytes increases over the spawning season (Hunter *et al.*, in press).

In central California 86% of the spawning biomass of Dover sole occurs along the upper continental slope between 600 m and 1000 m depth and some fish occur as deep as 1500 m (Hunter *et al.*, 1990). Their eggs are pelagic and occur at the surface as well as deeper in the water column. Thus, estimation of the biomass of this stock required development of methods for taking quantitative plankton tows from 1500 m to the surface.

In our example we use fish and egg data collected during trawl and ichthyoplankton surveys conducted from 1985 to 1988 (Butler *et al.*, 1989). We combine data from these years to reconstruct 4 months of the spawning season from December through April. The survey design varied between years: in 1987 we used a line transect design; in 1988 we used a random design stratified by bathymetric depth; and in 1985 and 1986 trawls were taken opportunistically and no plankton samples were taken. The survey area in each year was the same, and extended from Point Conception to Monterey Bay, California, an area of 14 172 km² (Fig. 1). This area is a small fraction of the total Dover sole habitat that extends from the Bering Sea to Baja California, Mexico (Eschmeyer *et al.*, 1983). Use of these historical data required two assumptions: the timing of the spawning season and the production of eggs were similar in 1985 to 1988 and no net transport of eggs occurs across the boundaries of the survey area.

We used 25–100 Dover sole from each trawl to estimate the four adult reproductive parameters (E, G, R, W). It was necessary to post-stratify the data by bathymetric depth because adult parameters changed markedly with depth (Hunter *et al.*, 1990). Each parameter was computed for each of the following area strata: stratum 1 was an area with bottom depth ≤ 456 m (249 fm), stratum 2 was 457–1004 m (250–549 fm) and stratum 3 was ≥ 1005 m (550 fm).

At each station in 1987 and 1988 we sampled Dover sole eggs with an oblique bongo tow retrieved from 210 m depth, and a deep oblique bongo tow which sampled the entire water column to a maximum of 1500 m depending on bathymetric depth. We attached a conductivity-temperature-depth (CTD) sensor to the deep bongo net to record depth and water temperatures every 20 seconds. The temperature varied from 5°C near the bottom to 15°C at the sea surface.

Estimates of egg production (P_o) are based on the full water column deep bongo tows but the comparison of egg

densities between deep bongo and 210 m bongo tows allowed us to allocate the eggs taken in each deep bongo tow into an upper segment (depth < 200 m) and lower segment (depth > 200 m) of the water column. This stratification was necessary because egg development rates are a function of temperature and temperature varies with depth. We used a temperature-dependent egg development model to assign ages to staged eggs on the basis of the mid-depth temperature in the upper 200 m segment and the lower depth segment of water column. Abundance of eggs at age was used to model egg mortality curve and to estimate egg production at age zero (P_o).

Results and discussion

The daily egg production ($P_o = 1.97/10$ m², CV=0.19) was computed from a Pareto survival function, and the daily population fecundity ($K = 0.28/g$, CV=0.15) was computed from a depth-stratified sampling design. The bootstrap method was used to compute the variance of each estimate (Lo *et al.*, in press).

To illustrate the magnitude of fecundity reduction, the daily decline in the standing stock of advanced yolked oocytes (total fecundity, G) and the daily decline in fraction of females with reproductively active ovaries (E) during a segment of the spawning season for stratum 2 (457–1004 m) are shown in Figures 2 and 3. In stratum 2 an active female spawns 255 eggs d⁻¹ and the fraction of the females with active ovaries is reduced by 0.5% d⁻¹. For example, if 60% of females were active at the beginning of January, 45% would be active at the end of January (Fig. 2). The parameter D_i can be also estimated by $(G_i E_i - G_{i+dt} E_{i+dt})/dt$ which would provide an estimate of the average rate of decline in daily fecundity for the season. This alternate method requires G and E to be estimated simultaneously for $G > 0$. We believe this alternate approach is disadvantageous because the sources of variability of G and E are masked. In addition, since the true form of the decline in G with time is likely to be non-linear, the estimate of the average rate for the season provided by the alternate method may have greater bias than estimates of the instantaneous rate at time t provided by our model.

The direct estimate of Dover sole biomass using equation (1) was 9971 mt (Table 1) with a coefficient of variation of 24%. The bootstrap estimate was 8725 mt with a coefficient of variation of 36%. The CV using the bootstrap method was higher than the direct method because the bootstrap estimate of P_o was more variable (Table 1). It appears that some upward bias may exist in the direct computation of K because the bootstrapped estimate (0.32) was higher than the direct computation (0.28). As a result, the bootstrap estimate (8725 mt) was different from one based on the direct computation (9971 mt). If the direct computation was corrected for

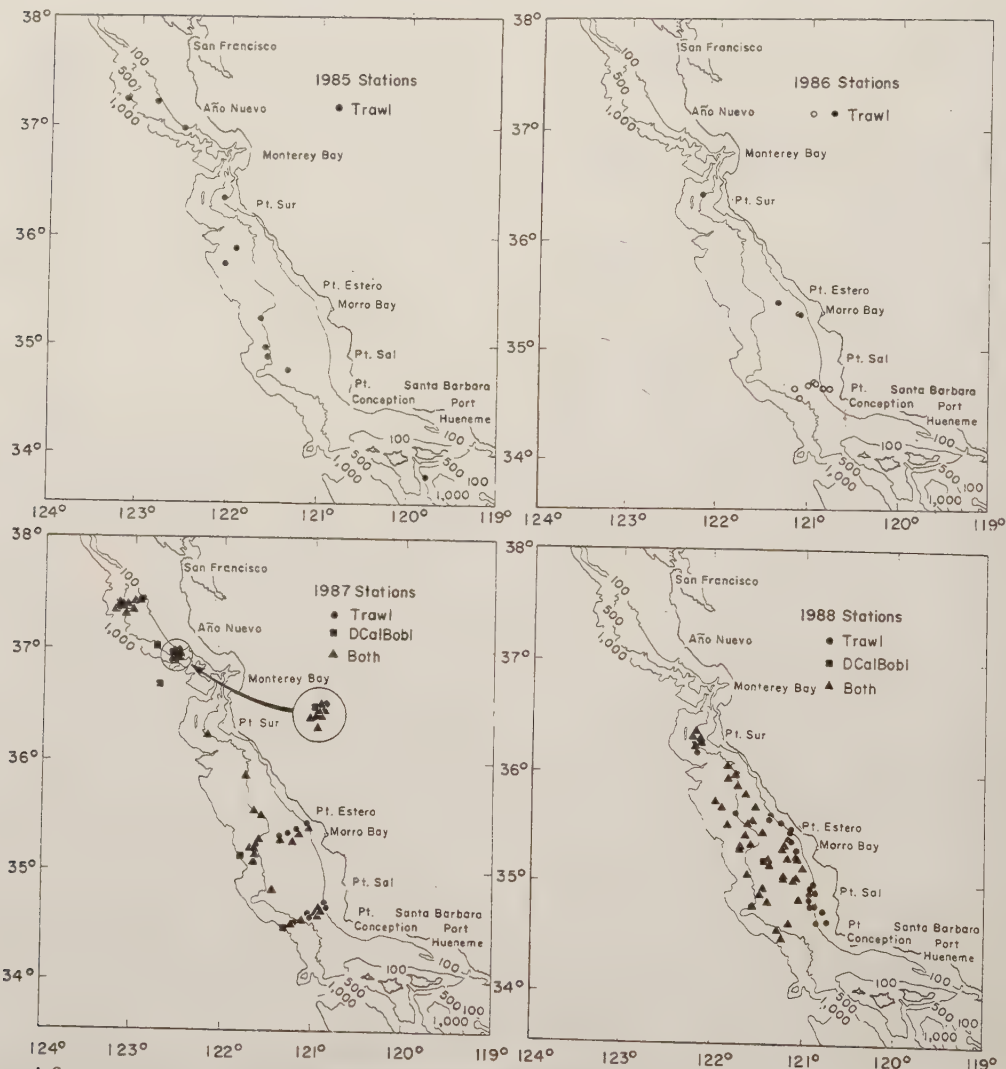


Figure 1. Survey patterns of Dover sole trawls and plankton tows in 1985–1988. In the 1986 survey open circles are stations occupied on cruise 8604, and solid circles are stations occupied on cruise 8606 (DCalBoli is deep bongo net tow).

this bias, the estimate (B_e) of biomass became 11 217 mt [$= 9971 - (8725 - 9971)$] ($CV = 0.51$) (Efron, 1982).

Abundance estimates for Dover sole in the same study area from trawl surveys range from 14 000 to 17 000 mt (Butler *et al.*, 1989). Thus, the DFRM estimate is close to the lower limit obtained by application of the swept area method to trawl catch data for the same area. Our estimates of biomass were probably too low because ichthyoplankton surveys did not extend to the offshore boundary of Dover sole eggs. Eggs were taken in the outermost stations of the survey pattern, indicating substantial offshore transport of eggs.

In addition to extending the offshore boundaries of our survey pattern, we need to improve our estimation of the ages of eggs. The temperature coefficient for incubation rates for Dover sole needs to be estimated in the laboratory. We also need to improve our method for assigning temperatures to eggs. We used the mean temperature over each of two depth ranges (depth < 200 m and depth > 200 m) to assign ages to the eggs taken in each of these ranges. This method underestimates the age of the eggs in the upper depth range since the eggs are spawned at the bottom and rise through the lower range before reaching the upper one. Although we believe the current method

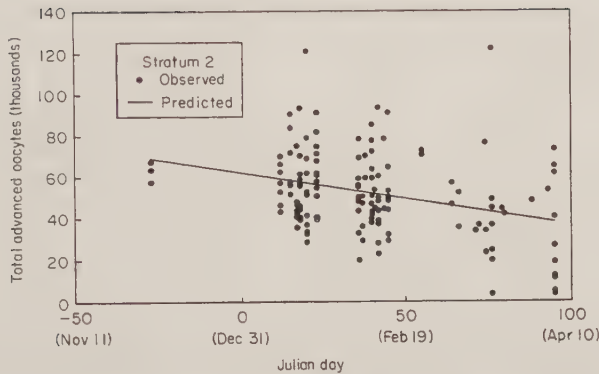


Figure 2. Decline in total advanced oocytes with time for stratum 2 (area with bottom depth 457–1004 m). Each point is one fish. Equation for the line showing the predicted value = $62.082 - 255.16$ Julian day.

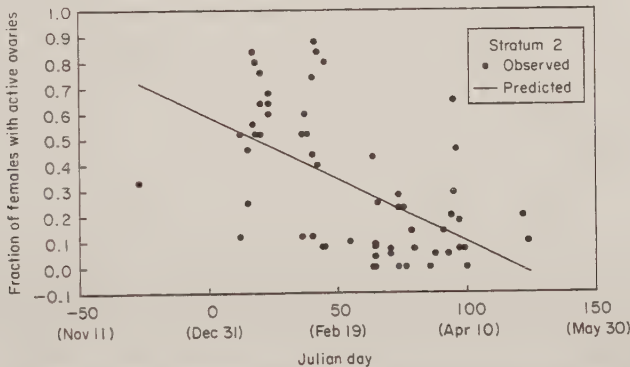


Figure 3. Decline in fraction of females with active ovaries with time for stratum 2 (area with bottom depth 457–1004 m). Each point is a trawl sample. Equation for the line showing the predicted value = $0.58 - 0.0049$ Julian day.

produces only a minor bias in the estimates of biomass, a temperature-dependent, vertical transit model for eggs would be preferable.

One of the chief advantages of the DFRM over the annual method was that sampling could be done over a short survey period. The DFRM does not require plankton samples be taken throughout the season as does the annual method so it may also save cruise time. Plankton sampling need not cover as long a period as we used in our example. In the example plankton samples were taken throughout a series of cruises spanning a period of 93 days, but a shorter period would be adequate for estimating P_0 . If P_0 was obtained from samples taken during a short period of time, D_t can be easily computed for the mid-point of that period. On the other hand, owing to the long spawning season of the Dover sole (5–6 months), and low batch fecundity, we needed an extended period to detect a change in fecundity (E) and the fraction of females with active ovaries (G). The fraction of females

with active ovaries declines only 15% per month and consequently a long time span is needed to detect a time dependent change in this variable. Our data indicate that 50 positive trawls (trawls in which some fish are caught) over a 100 day interval would provide an estimate of the daily rate of decline of the fraction active (G) with a coefficient of variation = 0.30. On the other hand, if the 50 positive trawls were taken over 30–40 days the coefficient for elapsed time is not detectable ($CV = 2.50$) (Lo *et al.*, in press). In many species having determinate fecundity, spawning seasons may be much shorter than the Dover sole. In such cases, probably a change in G could be detected during a short survey period.

Despite the problems with the available data, our example indicates that the DFRM is an appropriate method for estimating the biomass of Dover sole and other species of determinate fecundity. Formal application of the method to Dover sole would require that all samples be taken in the same year, that the offshore

Table 1. Estimates of parameters associated with adult reproduction of Dover sole, egg production (P_0), daily egg mortality (z) and biomass estimate (B) in central California by depth stratum 1985–1988¹.

Method ³	Depth stratum							
	0–456 (m) 0–249 (fm)		457–1004 (m) 250–549 (fm)		1005–1280 (m) 550–700 (fm)		Weighted mean ²	
	1	2	1	2	1	2	1	2
W (g)	250.53	253.22	776.07	763.7	1056.7	1063.5	668.51	659.5
S.E.	29.81	17.36	31.11	26.13	20.49	26.3	25.06	22.24
n	38		62		19			
R	0.67	0.7	0.76	0.79	0.92	0.85	0.74	0.78
S.E.	0.033	0.023	0.031	0.023	0.053	0.07	0.025	0.02
n	38		62		16			
$D_{50} = d(E \times G)/dt$	100.38	145.93	288.60	282.93	463.52	451.13	250.82	255.84
S.E.	26.98	33.88	61.63	22.64	92.68	50.83	48.41	18.52
n	37		60		16			
$k \times 10^{-6} = (R/W) \times D_{50}$	0.27	0.40	0.28	0.30	0.40	0.36	0.28	0.32
CV	0.30	0.23	0.182	0.07	0.21	0.14	0.15	0.09
A (area, km ²)	4049		7204		2919		total = 14 172	
Mean catch (lbs) per trawl	67.39		140.14		5.2			
Weighting factor	0.21		0.78		0.01			
$P_0/10 \text{ m}^2$	1.97	1.97						
S.E.	0.38	0.70						
β^4	0.6	0.54						
S.E.	0.10	0.17						
B (mt)	9971	8725						
CV	0.24	0.37						
B_c (mt)	11 217							
CV	0.51							

¹Abbreviations are as follows: W, the average female weight (g); R, female fraction of the population by weight; E, the total fecundity for average female weight; G, the fraction of females with yolked eggs; D_{50} , the number of eggs spawned per female per day for $t = 50$ (the mid-point of survey); $(R/W) \times D_{50}$, the daily population fecundity per gram; S.E., standard error; n, number of trawls. The biomass estimate (B) was computed based on equation (1). B_c is the bias-corrected biomass estimate.

²Weighted by the product of area and mean catch of trawl.

³Method 1 is the direct computation from formulas described in Lo *et al.* (in press). The standard error (S.E.) was from non-linear regression for P_0 , the jack-knife method for R and W, and formulas for D_{50} and K given in Lo *et al.* (in press). The S.E. of B was from equation (2). Method 2 is the bootstrap method.

⁴ β is the mortality coefficient in age dependent daily instantaneous mortality rate $z = \beta/(t + 1)$, where t is days.

boundary of the planktonic eggs be enclosed within the survey pattern and that planktonic eggs and adults be sampled contemporaneously.

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Indices of Relative Abundance from Fish Spotter Data based on Delta-Lognormal Models

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Fish spotters are pilots in small aircraft employed by commercial fishermen to locate, identify, estimate the size of, and direct boats toward pelagic fish schools. Data describing species, location, and size of schools can be inexpensively obtained from fish spotters but are difficult to interpret statistically. We developed an index of relative abundance from fish spotter data based on extended delta-lognormal models and applied the method to data for northern anchovy (*Engraulis mordax*). In contrast with previous approaches, our method used all available data, provided an index for northern anchovy that was proportional to abundance, and explicitly modeled factors (pilots, regions, seasons, and time of day) that affected observations by fish spotters. We also included information about mixed layer depth and sea surface temperature in models for a reduced study area and found that environmental data, where available, can be used to improve estimates of relative abundance from fish spotter data. Simulation results indicated that our approach is a cost-effective way to improve biomass estimates for pelagic species like northern anchovy.

Les observateurs de poissons sont des pilotes de petits avions employés par des pêcheurs commerciaux pour localiser, identifier, évaluer la taille et diriger les bateaux vers les bancs de poissons pélagiques. Des données indiquant l'espèce, l'emplacement et la taille des bancs peuvent être obtenues à peu de frais des observateurs de poissons, mais elles sont difficiles à interpréter statistiquement. Nous avons élaboré un indice d'abondance relative à partir des données des observateurs de poissons basé sur des modèles delta-lognormaux étendus et nous avons appliqué la méthode à des données sur l'anchois du Nord (*Engraulis mordax*). Contrairement à celles utilisées précédemment, notre méthode utilise toutes les données disponibles, fournit un indice pour l'anchois du Nord qui est proportionnel à l'abondance et modélise explicitement les facteurs (pilotes, régions, saisons et heure) qui influent sur les observations effectuées par les observateurs de poissons. Nous avons également inclus de l'information sur la température en surface et en profondeur des couches mélangées dans les modèles pour une aire d'étude réduite et nous avons découvert que les données environnementales, lorsque disponibles, peuvent être utilisées pour améliorer les estimations d'abondance relative faites à partir des données fournies par les observateurs de poissons. Les résultats des simulations ont indiqué que notre méthode constitue une façon économique d'améliorer les estimations de la biomasse d'espèces pélagiques comme l'anchois du Nord.

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Information about changes in abundance of fish stocks is an important part of information required for fisheries management. Catch-per-unit-effort (CPUE) data from fisheries have traditionally been used to measure changes in relative abundance, but accumulated evidence indicates that interpreting CPUE data from commercial fisheries is difficult, particularly for pelagic fish, because commercial CPUE data are affected by changes in fishing efficiency over time and tend to decline more slowly than abundance (Bannerot and Austin 1983; MacCall 1984). A number of alternative fishery-independent procedures for estimating relative abundance of fishes have been developed including scientifically designed acoustic surveys, trawl surveys, egg and larva surveys, aerial surveys, and tagging experiments (Ulltang 1977). These approaches may provide good results but are expensive. In contrast, aerial "fish spotters" are a potential source of large quantities of inexpensive information about relative abundance of pelagic fish that can be obtained from existing commercial operations. To date, fish spotter data have received relatively little attention from fishery managers.

Fish spotters are pilots in small aircraft employed by commercial fishermen to locate, identify, estimate the size of, and

direct boats towards pelagic fish schools (Squire 1961; Maughan and Marmelstein 1971). Fish spotters are used in the Australian southern bluefin tuna (*Thunnus maccoyii*) fishery; the southern California purse-seine fishery for northern anchovy (*Engraulis mordax*), Pacific (chub) mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), Pacific bonito (*Sarda chiliensis*), bluefin tuna (*Thunnus thynnus*), and Pacific sardine (*Sardinops sagax*); the South African purse-seine fishery for anchovy (*Engraulis capensis*) and pilchard (*Sardinops ocellata*); the Japanese sardine (*Sardinops melanostica*) fishery; the U.S. Atlantic menhaden (*Brevoortia tyrannus*) and swordfish (*Xiphias gladius*) fisheries, and other pelagic fisheries around the world (Squire 1961, 1972, 1983; Maughan and Marmelstein 1971; Agenbag 1980; Anonymous 1981; Williams 1981; Habib et al. 1982; Agenbag et al. 1984; Hara 1985).

It is important to emphasize the differences between data from fish spotters and data from aerial surveys conducted for scientific purposes. Methods are available for using data from scientifically designed aerial surveys, usually in connection with acoustic data, to estimate biomass or relative abundance of pelagic fishes (Cram and Hampton 1976; Rivas 1978; Hampton et al. 1979; Hara 1986; Scott et al. 1989; Hara 1990). Data

collected during such surveys are relatively easy to interpret but costly. In contrast, data collected opportunistically during the search for fishable schools by fish spotters are harder to interpret but inexpensive (Anonymous 1981).

Accuracy and precision of fish spotter data are reinforced because inaccurate species identification and poor estimates of school size inconvenience fishermen who employ fish spotters. Difficulties with interpretation of fish spotter data arise, however, because of factors that are unique to fish spotter data (imprecise nature of visual biomass estimates and differences among fish spotters) and other factors (patchy distribution of pelagic fish, lack of systematic sampling design, environmental variables, differences among regions, seasons, and time of day) that hinder interpretation of other types of data (e.g. commercial CPUE) as well. Flights are conducted only when environmental conditions are good enough for fishing, but environmental conditions still affect observations by fish spotters. Changes in fish spotters employed by a commercial fishery are another important problem because changes in abundance may be confounded by changes in fish spotters who collect the data. Despite problems in interpretation, fish spotter data can be useful and cost-effective tools for management purposes (Barnes et al. 1992), particularly, as in our analysis, when adjustments are made for differences among fish spotters, regions, and other important factors.

An important advantage of fish spotter data over commercial CPUE data is absence of saturation (increased abundance but no increase in CPUE due to limited hold capacity, trip limits for catch, market demand, or processing capacity) because fish spotters can record the size and location of all schools seen. This important characteristic makes it relatively easy to construct indices of abundance based on fish spotter data that are linear measures of fish biomass (i.e. change in proportion to biomass). Another advantage is that technical improvements to equipment used by fish spotters, such as aircraft and navigational gear, have probably not substantially increased their efficiency in locating fish. Fish spotters may purchase new aircraft and better navigational or radio equipment, but schools are still located visually while flying at reduced speeds and low altitudes. In contrast, changes in commercial CPUE due to changes in fish abundance are often confounded by technical improvements to fishing gear such as nets and acoustic equipment (Kimura 1981; Jacobson et al. 1987).

We developed delta-lognormal linear models (Shimizu 1988) for fish spotter data based on the delta distribution (Aitchison and Brown 1957; Pennington 1983) and lognormal linear models (Bradú and Mundlak 1970; Kerlinger and Pedhazur 1973; McCullagh and Nelder 1983). Our approach extends delta-lognormal models and breaks new ground in fisheries because we model components of the delta distribution as functions of factors and covariates in lognormal linear models (Lambert 1992) and provide approximate variances for estimates. Lognormal linear models are similar to analysis of variance models fit using linear regression and often used by fishery scientists and managers to derive a single index of fishing effort for a group of heterogeneous vessels or to derive a single index of relative abundance for a fish stock from two or more types of data (Gulland 1956; Robson 1966; Kimura 1981, 1988; MacCall and Prager 1988; Hilborn and Walters 1992). Although we used lognormal linear models for components of the delta distribution, other linear or nonlinear models based on other statistical distributions could be used instead.

The delta distribution is often used to estimate abundance of planktonic organisms whose spatial distribution is highly con-

tagious (Dennis and Patil 1988). Survey data for planktonic organisms typically have statistical distributions with a large fraction of "zeros" (samples in which no organisms are observed) and may be so distorted that conventional methods based on the sample mean yield inefficient estimates of abundance. The delta distribution avoids problems with contagion by treating zero and nonzero data separately; final estimates of abundance are obtained from the product of the proportion and mean for nonzero observations. The delta distribution is used in many disciplines to model processes that generate more zero observations than might be expected on the basis of distributional assumptions (Lambert 1992).

Our approach used two lognormal linear models: the first to estimate the proportion of flights in which fish were seen by fish spotters and the second to estimate density (tons per area) of fish from data for flights during which fish were seen. Analogous to the delta distribution, our index of relative abundance from fish spotter data was based on the product of these quantities (adjusted for the size of the survey area as described below).

We applied our models to data for northern anchovy off the coast of southern California. In addition, we applied an expanded version of the model to a subset of the fish spotter data and two environmental variables (sea surface temperature and mixed layer depth) to determine if environmental information could potentially be used to improve estimates. Other types of environmental data (e.g. sea state and wind speed) were not available but may have been useful. The amount of data available and models used in our analysis enabled us to obtain useful estimates from fish spotter data and to account for differences among fish spotters, regions, seasons, time of day, and other variables.

Previous analyses of fish spotter data used a simple CPUE-like index (tons sighted per block area flight or T/BAF) to measure relative abundance (Squire 1961, 1972, 1983). The T/BAF index was corrected for time of day by excluding data for day flights and corrected for differences among regions by restricting the analysis to a "core" region where the species of interest was naturally abundant. A significant advance in our analysis was that all available information was used to estimate abundance; corrections for differences between time of day, among regions, and seasons were made without excluding data.

Another important difference between our analysis and previous ones was that we made corrections for differences among fish spotters. Our records indicated consistent differences among fish spotters in mean reported weight of anchovy schools and the proportion of flights during which schools were sighted (Fig. 1). Moreover, fish spotters participating in the monitoring program changed over time so that, for example, some fish spotters participated only during the 1960's and 1970's, while others did not begin to participate until the late 1980's. If indices of abundance from fish spotter data were not corrected for differences among fish spotters, then temporal changes in abundance may have been confounded by changes in fish spotters. As shown below, effects of fish spotters were important for anchovy.

The original motivation for our work was to improve spawning biomass estimates used to manage the fishery for northern anchovy. Data for biomass estimates were reduced in recent years and precision and accuracy of biomass estimates deteriorated (Jacobson and Lo 1990). For this reason, we conducted simulation experiments to determine if our new index based on fish spotter data could be used to improve biomass estimates and management advice for northern anchovy.

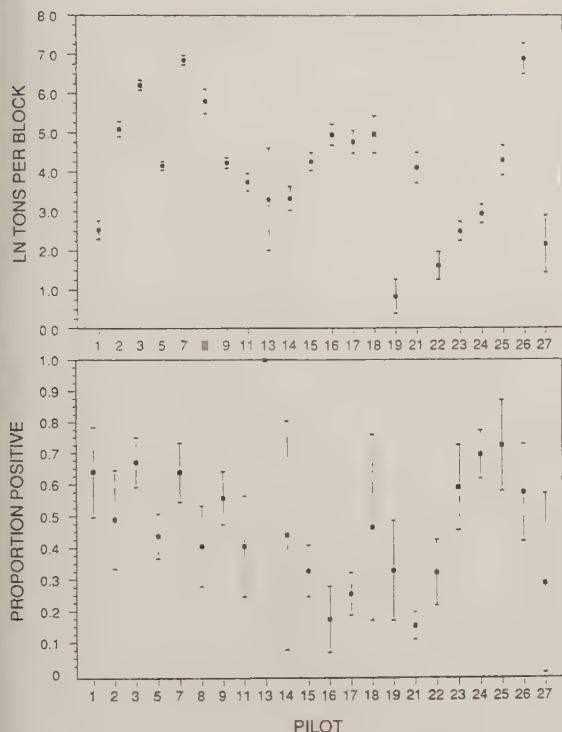


FIG. 1. Mean log tons of anchovy sighted per block (top panel) and proportion positive blocks (bottom panel) for fish spotters in region 2 (see Fig. 2) during 1963–90. Some fish spotters did not participate during the entire time period. Vertical bars show means ± 2 SE.

Materials and Methods

The anchovy data used in our analyses were collected by fish spotters paid a nominal wage (\$1 to \$4 per hour) to participate in a pelagic resource monitoring program initiated in 1962 by the Tiburon Marine Laboratory, U.S. Fish and Wildlife Service (now Southwest Fisheries Science Center, National Marine Fisheries Service, or NMFS), in central and southern California (Squire 1961, 1972). Data were collected during the course of routine fish spotting and involved little additional effort by fish spotters. The data set (called the “complete” data set below) included records from about 16 000 flights conducted during 1963–90 (records for fish spotters with less than 20 flights were omitted). The subset of fish spotter data used with environmental data consisted of records from about 3700 flights over a smaller geographic area (records for fish spotters with less than 10 flights were omitted).

Fish spotters recorded the species (most pelagic schooling fishes of commercial importance can be identified from the air), location, time of day, and estimated weight of all fish schools encountered during flights in special flight logs (Squire 1961, 1972). Locations were specified by “blocks” which are 10' latitude by 10' longitude. Time of day was either day or night (fish schools are visible at night due to bioluminescence; Squire 1972). Flight log data for each sighting were checked for errors and entered into a computer database.

The area covered by fish spotters was divided into six regions (Fig. 2). During 1963–90, fish spotters collected data from the area between 27 and 37°N latitude, but anchovy were most common in the area north of region 6 (30°33'N latitude). Data for region 6 were excluded from our analysis because anchovy were seldom seen there.

Sea surface temperature and mixed layer depth were estimated for each block using data collected during routine California Cooperative Oceanic Fisheries Investigations (CalCOFI) research cruises (L. Eber, NMFS, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA, 92038 USA, pers. comm.). CalCOFI cruises were conducted throughout the study period (with some interruptions) on a quarterly basis (Hewitt 1988). Environmental data could be obtained for regions 2 and 3 (Fig. 2) only because CalCOFI cruises have been limited to these regions since 1987. Years with no CalCOFI environmental data were omitted from our models when environmental data were included.

Sea surface temperature and mixed layer depth were treated as categorical, rather than continuous, variables because initial estimates of the functional form of the relationships between anchovy biomass and sea surface temperature or mixed layer depth were erratic when environmental data were treated as continuous variables. Although preliminary estimates of functional forms were uninterpretable, it was clear that anchovy abundance varied with sea surface temperature and mixed layer depth when the environmental data were treated as categorical variables. Sea surface temperature data were, therefore, aggregated in 2°C categories and mixed layer depth data were aggregated into 20-m categories. Intervals for the categories were chosen so that there was a sufficiently large number of observations in each category.

Models

As described above, relative abundance of northern anchovy was expressed as the product of density and a measure of area:

$$(1) \quad I = DA$$

where I is the index of relative abundance for a given year (tons), D is density of anchovy (tons per block), and A is the area (blocks) covered by fish spotters. We assumed that fish spotters flew over an area that was at least as large as the area occupied by the anchovy stock in each year. Units for the index (I) are tons of anchovy sighted by fish spotters.

Density of anchovy (D) for each year was

$$(2) \quad D = dP$$

where d is a standardized measure of anchovy density (tons per block) for positive flights (flights during which anchovy were seen) and P is a standardized measure of the proportion of blocks that were covered by positive flights (referred to as proportion positive). As described above, density of anchovy (D) was calculated from the product of density in positive blocks (d) and proportion positive (P) in order to avoid problems that arise from including a large number of zeros. Moreover, area of the stock (A), density for positive flights (d), and proportion positive (P) are all useful measures of relative abundance for pelagic species (MacCall 1990; Mangel and Smith 1990; Smith 1990), while area (A) and proportion positive (P) provide information about spatial distribution.

The complete data set was used to obtain standardized estimates of anchovy density for positive blocks (d) and proportion positive (P) for each year using lognormal linear models

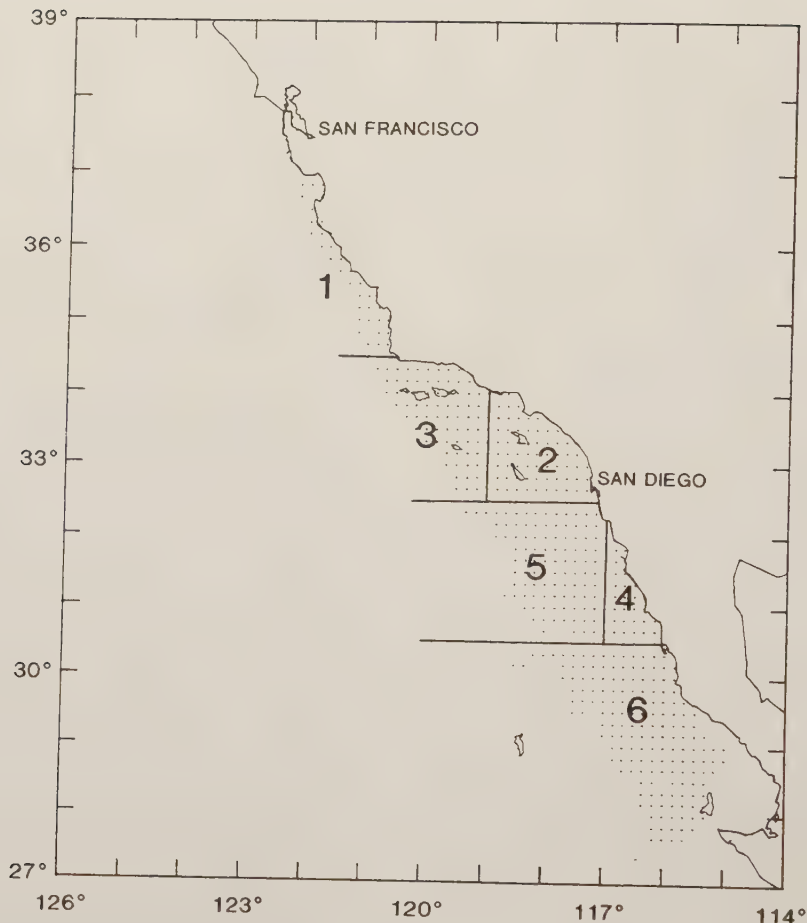


FIG. 2. Study area, regions, and blocks covered by fish spotters in 1989. Regions are outlined and denoted by numbers. Blocks are denoted by dots.

described below. Five factors were treated as main effects: years, fish spotters, regions, seasons, and time of day (day or night). Factors were allowed to cross in the model so that any combination of years, fish spotters, regions, seasons, and time of day could be accommodated. In addition to main effects, first-order interactions between regions, seasons, and time of day were included in the models. Other first-order and higher order interactions were not included to avoid overparameterization of models and problems with parameter estimation as well as to limit the amount of computer memory required.

Data used to estimate density of anchovy for positive flights (d) were aggregated by flight. The model was

$$\ln(d) = X\beta + Z\alpha + \epsilon$$

where d is a vector for observations, X is the design matrix for main effects and β is the parameter vector for main effects, Z is the design matrix for interactions and α is the parameter vector for interactions, and ϵ is a vector of independent normally distributed errors with expectation zero and variance σ^2 .

For record k , we have

$$(3) \ln(d_k) = \ln(y_k/b_k) = f(\beta, \alpha, X_k) + \epsilon_k$$

and

$$(4) f(\beta, \alpha, X_k) = \beta_0 + \sum_{i=1}^5 \sum_{w=1}^{J_i} \beta_{iw} X_{iwk} + \sum_{i=1}^5 \sum_{w=1}^{J_i} \sum_{L=1}^5 \sum_{v=1}^{J_L} \alpha_{iwlv} X_{iwlv} X_{Lvk}$$

where d_k is tons of anchovy sighted per block for positive flight k , b_k is the total number of blocks searched during positive flight k (not the number of positive blocks), y_k is total tons of anchovy sighted, and ϵ_k is a normally distributed error with expectation zero and variance σ^2 . The number of positive blocks (b_k) was incremented each time a fish spotter left one block and entered another so that an individual block searched twice during a flight would be counted twice.

Subscripts i and L in (4) index main effects (years, fish spotters, regions, seasons, and time of day), w and v index factor levels (e.g. spring, summer, and autumn for seasonal effects), J_i is the number of levels for factor i , J_L is the number of levels for factor L , and k is used to index flights or records. The coefficient β_0 is the mean log density ($\ln(d_k)$) of anchovy sighted

TABLE 1. Symbols and descriptions for main effect and interaction parameters in lognormal linear models. The symbols "w" and "v" are used to subscript factor levels. The symbols "α" and "β" are used in models for density, while "γ" and "τ" are used in models for proportion positive.

Parameter	Description
α or γ	Vector for interaction parameters
β or τ	Vector for main effect parameters
β ₀ or τ ₀	Mean log density (ln(<i>d_i</i>)) or mean log proportion positive (ln(<i>P_k</i> + 1)) of anchovy sighted for a reference year (1963), region (region 2), season (winter, January–March), time of day (nighttime), fish spotter (fish spotter 1), and, if applicable, set of environmental conditions
β _{1w} or τ _{1w}	Year effects; <i>w</i> = 1–27 for years 1964–90
β _{2w} or τ _{2w}	Region effects; <i>w</i> = 1–4 for regions 1, 3, 4, and 5
β _{3w} or τ _{3w}	Seasonal effects; <i>w</i> = 1–3 for spring (April–June), summer (July–September), and autumn (October–December)
β _{4w} or τ _{4w}	Day/night effect; <i>w</i> = 1 for daytime
β _{5w} or τ _{5w}	Fish spotter effects; <i>w</i> = 1–21 for fish spotters numbered 2–27 (some fish spotters with less than 20 flights excluded)
β _{6w} or τ _{6w}	Temperature effects; <i>w</i> = 1–4 for temperatures ≤12°C, >12 and ≤14°C, >16 and ≤18°C, and >18°C
β _{7w} or τ _{7w}	Mixed layer depth effects; <i>w</i> = 1–3 for mixed layer depths ≤20 m, >20 and ≤40 m, and >60 m
α _{2w3v} or τ _{2w3v}	Interaction between regions and seasons; <i>w</i> = 1–4 and <i>v</i> = 1–3
α _{3w4v} or τ _{3w4v}	Interaction between seasons and time of a day; <i>w</i> = 1–3 and <i>v</i> = 1
α _{2w4v} or τ _{2w4v}	Interaction between regions and time of a day; <i>w</i> = 1–4 and <i>v</i> = 1

for a reference year (1963), region (region 2), season (winter, January–March), time of day (nighttime), and fish spotter (fish spotter 1). The vectors β and α hold parameters for main effects and interactions (see Table 1 for details). The vector *X_k* holds the dummy variables *X_{iwk}* (Weisberg 1980) for main effect *i*, level *w*, and positive flight *k*. The number of parameters and dummy variables for each main effect was equal to the number of categories minus 1. There were, for example, three parameters for seasonal effects with three dummy variables that were 0,0,0 for winter (January–March) flights, 1,0,0 for spring (April–June) flights, 0,1,0 for summer (July–September) flights, and 0,0,1 for autumn (October–December) flights.

We used a stepwise linear regression program (BMDP2R; Dixon et al. 1988) to obtain maximum likelihood estimates for parameters in (3) and (4). The stepwise regression program sequentially applied forward selection and backward elimination algorithms to avoid problems associated with using one or the other exclusively (Weisberg 1980; Draper and Smith 1981), and statistical significance was established if the *F*-value for parameters associated with a main effect or interaction exceeded 4.0. The stepwise regression program made it easy for us to identify and select groups of parameters for main effects and

interactions in the model that were statistically significant (i.e. explained a significant amount of variance in the dependent variable; see Kerlinger and Pedhazur 1973). In a few cases, we forced the program to include an insignificant main effect or effects associated with a significant interaction so that, for example, both main effects A and B would be included if the interaction between A and B was significant. Changes in the coefficient of determination (*R*²) and order in which the stepwise regression procedure included variables and interactions were used as crude measures of their relative importance.

A standardized and unbiased measure of anchovy density in positive flights during year *j* is $\hat{d}_j = \exp(\beta_0 + \beta_{1j} + \sigma^2/2)$ where β₀ is mean log density (ln(*d_i*)) for the reference year, region, season, time of day, and fish spotter and β_{1j} is the main effect for year *j*. This measure was estimated by

$$(5) \hat{d}_j = \exp(\hat{\beta}_0 + \hat{\beta}_{1j}) \Psi_{d_j}$$

where "hats" (̂) denote estimates from fitting the lognormal linear model (3) to data and Ψ_{*d*} is a correction for bias. The correction for bias and variance of $\hat{d}_j$ were calculated as described in Appendix 1.

Data used to estimate proportion positive (*P*) were aggregated by year, fish spotter, region, time of day, and season in order to reduce the size of the data set. Preliminary analyses indicated that effects of different approaches to aggregating data were minimal. A lognormal linear model similar to (3) and (4) was used to estimate proportion positive:

$$(6) \ln(P_k + 1) = \ln(f_k/B_k + 1) = f(\tau, \gamma, X_k) + \zeta_k$$

where *P_k* is proportion positive for record *k*. Positive blocks (*f_k*) is the total number of blocks searched during positive flights and *B_k* is the total number of blocks searched during all flights that contribute to record *k*. The additive constant 1 in (6) allowed logarithmic transformation when *P_k* was zero. Choice of additive constant can effect results from analysis of variance models (Berry 1987). The additive constant 1 was a reasonable choice for our data because it usually reduced and never increased skewness after the transformation, while smaller values (e.g. 0.1) sometimes increased skewness. The linear function *f*() in (6) is the same as in (3) and (4) except that the vectors τ and γ hold parameters for main effects and interactions (Table 1). The term ζ_{*k*} was assumed to be a normally distributed error with expectation zero and variance δ².

The assumption of normally distributed errors (ε_{*k*} and ζ_{*k*}) in (3) and (6) was reasonable because of the Central Limit Theorem (values of *P_k* were averages usually computed from a large number of observations) and because scatter diagrams of residuals were symmetric. A natural alternative would have been to assume binomial-distributed errors and estimate proportion positive (*P_k*) by logistic regression or other likelihood-based procedures (McCullagh and Nelder 1983). We chose to assume normally distributed errors because software for lognormal linear models facilitated computation of approximate variances for proportion positive and our index of relative abundance (Appendix 1). The assumption of constant variances in (3) and (6) was reasonable because scatter diagrams of residuals did not show any trend when plotted against predicated values or independent variables.

A standardized and unbiased measure of proportion positive during year *j* is $\hat{P}_j = \exp(\tau_0 + \tau_{1j} + \delta^2/2) - 1$ where τ₀ is the mean of log proportion positive (ln(*P_k* + 1)) for a reference year, region, season, time of day, and fish spotter and τ_{1j} is the main effect for year *j*. This measure was estimated by

$$(7) \hat{P}_j = \exp(\hat{\tau}_0 + \hat{\tau}_{1j}) \Psi_{\hat{P}_j} - 1$$

where Ψ_p is a correction for bias and estimates were obtained by fitting the lognormal linear model (6) to data. The correction for bias and variance of $\hat{P}_j$ were calculated as described in Appendix 1.

Substituting (2) into (1) and replacing parameters with their estimates from (5) and (7) gives the following estimate of relative abundance for anchovy in year j :

$$(8) \quad \hat{I}_j = \hat{d}_j \hat{P}_j A_j \\ = [\exp(\hat{\beta}_0 + \hat{\beta}_{1j}) \Psi_{\hat{d}_j}] [\exp(\hat{\tau}_0 + \hat{\tau}_{1j}) \Psi_{\hat{P}_j} - 1] A_j.$$

Variance of (8) was estimated as described in Appendix 1. Models and procedures used with environmental and fish spotter data were similar to those used with the complete data set.

The structure of models (3) and (6) allowed us to estimate abundance of anchovy in the last year of the time series from data for only one season in that year. The estimates obtained in our analysis for 1990, for example, were based on data for January–March, while estimates for all other years were based on data for January–December. Use of data for one season or partial season in the last year decreases precision but makes it possible for managers to make estimates, which may be important in some circumstances, of relative abundance during the most recent or current fishing season. Another approach is to use annual periods other than calendar years so that the last season with data is the end of the last annual period (Jacobson and Lo 1991).

Results and Discussion

For the complete data set, the stepwise regression procedure included the same variables and interaction terms in the model (3) for density (d) and as in the model (6) for proportion positive (P) (Table 2). Effects due to time of day, regions, seasons, and fish spotters were all more pronounced than year effects (which are used in (8) to estimate relative abundance) in both models (Table 2). Final estimates for all indices (corrected for bias) are given with standard errors in Table 3.

Results for the environmental and subset of the fish spotter data were similar to those for the complete data set except that

the stepwise regression procedure included sea surface temperature in the model (3) for density (d) and both temperature and mixed layer depth in the model (6) for proportion positive (P). Although effects due to sea surface temperature and mixed layer depth were less pronounced than year effects in both models, these results indicate that environmental data were useful in interpreting fish spotter data. Final estimates for all indices (corrected for bias) are given with standard errors in Table 4.

Additional information about the importance of environmental variables can be obtained by examining results for 1983 which was an El Niño year with unusually warm water temperatures in the study area (Fiedler et al. 1986). The estimate of relative abundance (I) for anchovy during 1983 from the complete data set was implausibly low relative to the estimates for 1981, 1982, and 1984 due to low density (d) and proportion positive (P) (Fig. 3; Table 3), while the coefficient of variation (CV) for 1983 was higher than for adjacent years (Table 3). In contrast, the estimate of relative abundance (I) during 1983 and the coefficient of variation from fish spotter and environmental data (Fig. 3; Table 4) were more similar to estimates for 1981 and 1984 (no estimate for 1982 was available because of no environmental data). This result indicates that environmental data may be important in interpreting fish spotter data, particularly, as in El Niño years, when unusual environmental conditions exist.

Total area covered by fish spotters in each year (A) increased from 180 blocks in 1963 to around 350 blocks in the late 1980's (Table 3; Fig. 4). The number of blocks in which anchovy were sighted averaged about 100 blocks during 1963–84 and about 150 blocks during 1985–90. Since the number of blocks covered by fish spotters in each year was larger than the number of blocks in which anchovy were seen, we concluded that there was little bias in our estimates of relative abundance (I) due to fish spotters failing to cover the entire range of the anchovy stock.

Evaluation of Indices

We evaluated indices of relative abundance from fish spotter data by comparing them with estimates of total anchovy bio-

TABLE 2. Summary of lognormal linear models for density in positive blocks (d) and proportion positive (P) fit to the complete fish spotter data set for northern anchovy. Columns give the order of entry and change in R^2 for main effects and interactions included in the models. Numbers in parentheses indicate the number of parameters estimated for each variable or interaction. The row labeled "Records" gives the total number of flights (in the model for density) or records (in the model for proportion positive) used to estimate parameters.

	Density (d)		Proportion positive (P)	
	Order	Change in R^2	Order	Change in R^2
Intercept				
Time of day	1	0.088 (1)		
Regions	3	0.028 (4)	3	0.0016 (1)
Fish spotters	2	0.26 (21)	1	0.056 (4)
Seasons	5	0.0127 (3)	4	0.105 (21)
Years	6	0.058 (27)	2	0.025 (3)
Region by time			5	0.058 (27)
of day interaction				
Season by time	4	0.0217 (3) ^a	6	0.0172 (4)
of day interaction				
Region by season	8	0.0016 (3)	7	0.009 (3)
interaction				
Records	7	0.015 (10) ^a	8	0.011 (10) ^a
Total R^2 (adjusted)	6793	0.48	3733	0.24

^aSome coefficients were not estimated because of collinearity with other independent variables.

TABLE 3. Relative abundance of anchovy during 1963–90 and other estimates from the complete fish spotter data set. *A* is the area (number of unique blocks) covered by fish spotters in each year, number positive is the number of blocks in which anchovy were seen, *d* is density (tons per block) of anchovy for positive flights, *P* is proportion positive, *I* is relative abundance of anchovy, and CV is the coefficient of variation. Estimates of density (*d*) and proportion positive (*P*) were corrected for bias as described in the text.

Year	A	Number positive	<i>d</i> ^a	CV(<i>d</i>)(%)	<i>P</i>	CV(<i>P</i>)(%)	<i>I</i>	CV(<i>I</i>)(%)
1963	180	126	13	22	0.47	15	1 129	27
1964	206	118	76	26	0.61	16	9 569	30
1965	208	112	67	25	0.56	17	7 851	31
1966	224	106	109	24	0.60	16	14 643	29
1967	200	108	132	23	0.72	14	19 105	27
1968	221	106	50	25	0.48	19	5 260	31
1969	223	90	163	23	0.51	18	18 663	29
1970	143	75	167	24	0.71	16	16 965	29
1971	175	82	156	23	0.70	15	19 082	27
1972	184	87	154	23	0.67	16	19 025	28
1973	338	146	339	23	0.64	15	73 493	28
1974	304	96	255	23	0.76	14	58 892	27
1975	280	68	392	23	0.84	14	91 789	27
1976	388	97	221	23	0.63	16	53 966	28
1977	289	99	248	23	0.71	15	50 683	27
1978	283	84	358	25	0.52	18	52 898	31
1979	288	88	590	25	0.54	19	91 366	31
1980	196	100	455	29	0.69	19	61 345	34
1981	232	110	313	29	0.46	23	33 281	37
1982	249	88	264	28	0.42	24	27 846	37
1983	340	79	78	36	0.27	33	7 125	49
1984	341	82	176	32	0.29	31	17 373	45
1985	357	151	349	30	0.44	22	54 261	38
1986	332	122	132	29	0.42	23	18 289	38
1987	352	119	114	31	0.43	24	17 103	40
1988	335	201	275	31	0.50	22	46 164	38
1989	379	142	81	32	0.47	23	14 373	40
1990	351 ^b	147 ^b	227	42	0.41	33	32 527	54

^aRounded to nearest integer.

^bArea (*A*) and number positive for 1990 estimated from the average values for 1985–89.

mass during 1964–86 (Fig. 3) obtained independently by catch-at-age analysis using a stock synthesis model (Methot 1989). The stock synthesis model is a form of catch-at-age analysis that incorporates information about relative abundance of spawning or schooling anchovy from four fishery-independent surveys, commercial fishery data, and environmental data in a single maximum likelihood based procedure. Although the stock synthesis model for northern anchovy was designed to estimate spawning biomass, total biomass estimates are produced as well (Methot 1989; Lo and Methot 1989). Stock synthesis estimates of anchovy biomass have been used to set catch quotas since 1986 and were the best estimates available.

We also compared our estimates of relative abundance with updated versions of the simple T/BAF index from fish spotter data (Fig. 3) described by Squire (1972, 1983) to determine if our more complex approach was any better.

When comparing indices, it is important to remember that estimates of relative abundance from fish spotter data measure changes in *schooling* biomass rather than total, catchable, or spawning biomass. These distinctions may be important if, for example, young fish do not school or a large fraction of the stock is immature.

The first step in evaluating indices was to determine which were linear measures of relative biomass for northern anchovy. We fit a quadratic polynomial (parabolic) regression model to each index of relative abundance:

$$(9) \quad L_y = \iota_1 B_y + \iota_2 B_y^2 + \epsilon_y$$

where L_y is an index that measures biomass in year *y* (e.g. T/BAF), B_y is anchovy biomass during year *y* estimated by Methot (1989) using a stock synthesis model, ι_1 and ι_2 are parameters, and ϵ_y is a normally distributed statistical error. The important features of this model are that it intersects the origin (indices have zero value at zero anchovy biomass) and nonlinearity in the relationship between an index and anchovy biomass is indicated by the sign and statistical significance of the estimate of ι_2 . If the index of abundance (L) is not a linear estimate of anchovy biomass (B), then the estimate of ι_2 should be significantly different from zero. Negative values of ι_2 indicate saturation. The parabolic model (9) worked well for our data because the inflection point of the fitted line fell outside the range of the data for each index and the line was always increasing in the range from zero to the largest observed biomass level.

Results from the regression analyses (Table 5) indicate that our index of relative abundance from fish spotter data (*I*) and T/BAF were linear measures of relative anchovy biomass (Table 5). Parameter estimates for ι_2 were not statistically significant (p -value > 0.05) for our index of relative abundance from fish spotter data (*I*, with and without environmental data), T/BAF, and, in the case of fish spotter with environmental data, proportion positive (*P*).

To further evaluate linear measures of relative biomass for anchovy, we computed correlation coefficients between indices from fish spotter data and stock synthesis estimates of anchovy biomass:

TABLE 4. Relative abundance of anchovy during 1963–90 and other estimates from a subset of the complete fish spotter data plus environmental data. Column headings and definitions as in Table 3. Area (A in (8)) used to estimate relative abundance from fish spotter and environmental data was the same as listed in Table 3 for a complete data set. Estimates for some years are unavailable due to a lack of environmental data.

Year	d^a	CV(d)(%)	P	CV(P)(%)	I	CV(I)(%)
1963	41	33	0.19	9	1 366	34
1964	532	43	0.16	14	17 452	45
1965	368	45	0.16	15	12 076	47
1966	864	35	0.15	12	29 311	37
1967	820	40	0.17	13	28 634	42
1968	245	40	0.08	25	4 126	48
1969	943	33	0.13	13	27 583	36
1970						
1971						
1972	810	35	0.13	13	19 449	37
1973			No environmental data available			
1974	819	37	0.30	9	74 747	38
1975	2 564	34	0.25	8	179 773	35
1976	676	41	0.10	25	26 526	48
1977	645	40	0.11	21	20 911	46
1978	1 804	39	0.06	30	29 046	49
1979	1 153	77	0.06	48	19 729	91
1980	1 809	57	0.17	19	60 890	60
1981	1 057	52	0.11	22	26 877	56
1982						
1983	520	57	0.03	75	5 389	94
1984	562	57	0.04	57	8 387	81
1985	891	56	0.05	50	16 123	76
1986	794	57	0.05	52	12 687	77
1987	868	57	0.05	53	14 566	78
1988	434	63	0.02	129	3 166	144
1989	2 052	67	0.06	46	45 568	81
1990	1 445	63	0.07	48	33 333	79

^aRounded to nearest integer.

Index	Correlation with stock synthesis estimates
T/BAF	0.60
I (no environmental data)	0.67
I (with environmental data)	0.63

Indices of relative abundance (I) for anchovy based on delta-lognormal linear models appear superior to the T/BAF index because correlations with stock synthesis estimates of total biomass were slightly higher and because the T/BAF index dropped to implausibly low levels after 1982 (Fig. 3).

The correlation between stock synthesis estimates of biomass and our estimates of relative abundance (I) from environmental plus fish spotter data was almost as good as the correlation with estimates from the complete data set even though the sample size for each year was smaller. This result indicates that environmental data, if readily available, could be used to improve the precision of relative abundance indices from fish spotter data.

Simulation of Anchovy Biomass Estimates

Two simulation experiments involving the stock synthesis model for anchovy were conducted to determine if our index of schooling biomass (I) could be used to improve spawning stock biomass estimates for northern anchovy. The stock synthesis model was used in the simulation experiment because it was convenient and actually used to manage anchovy, but any

other type of catch-at-age analysis with auxiliary information (Deriso et al. 1985; Pope and Shepherd 1985; Gavaris 1988) would have been just as suitable. Our results are general enough to indicate the relative benefits of including fish spotter data in catch-at-age analysis with auxiliary information for fisheries similar to the anchovy fishery. A detailed description of the simulations is given in Appendix 2.

Simulation results indicated that fish spotter data increased the precision of biomass estimates from the stock synthesis model by about 10% on average (Fig. 5). Coefficients of variation for spawning biomass estimates with fish spotter data ranged from 7.8 to 40% in the last year and ranged from 7.6 to 54% in the last year without fish spotter data.

Fish spotter data may have reduced bias in stock synthesis estimates of spawning biomass for northern anchovy. Bias of stock synthesis estimates for each year was measured by the percentage difference between the mean estimate from the simulations and the "true" value assumed in the simulation experiment, i.e. as $(I_{\text{average}} - I_{\text{true}})/I_{\text{true}} \times 100$. Percentage difference is a reasonable measure of bias when the number of simulations employed is large but may be misleading when the number of simulations is as small as 50 because the mean of a small sample will differ from the underlying population mean due to sampling error only (Efron 1982).

The absolute value of our measure of bias ranged from 0 to 10% (0–63 000 tons) of true values in the simulation for relative abundance estimates from fish spotter data and from 0 to 12% (0–75 000 tons) for relative abundance estimates without fish spotter data (Fig. 5). As explained above, however, these

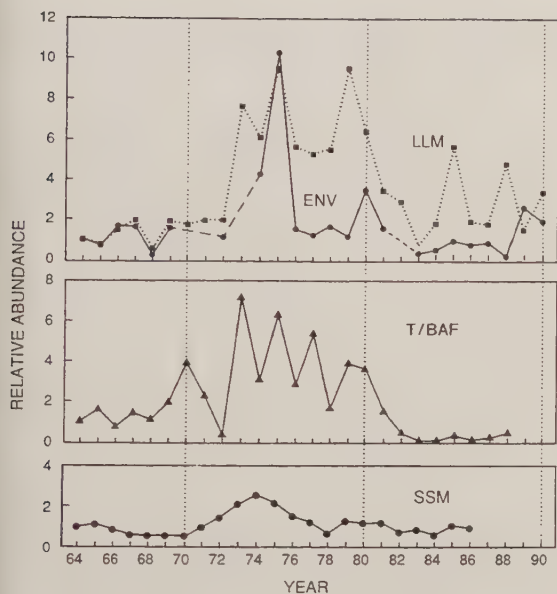


FIG. 3. Stock synthesis model (SSM) estimates of total biomass (Methot 1989), a catch-per-unit-effort-like index (T/BAF) from fish spotter data (revised and updated values similar to data given in Squire 1972), and estimates of relative abundance from delta-lognormal linear models fit to fish spotter data with (ENV) and without (LLM) environmental data. Before plotting, each series was scaled so that the value of 1964 was equal to 1.0 (i.e. the values in each series were divided by the value for 1964).

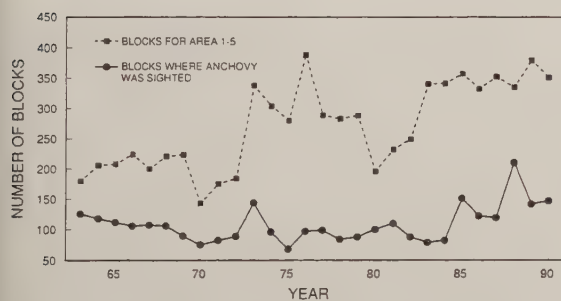


FIG. 4. Number of blocks in regions 1-5 covered by fish spotters (A) and number of blocks where anchovy were found during 1963-90.

results were based on relatively few simulations and may be misleading. Additional work is required to determine the nature and extent of possible bias in the stock synthesis model.

The most important effect of using fish spotter data in the simulations was increased precision and potential reduction in bias for the last year's estimate. The biomass estimate for the last year is the least precise in most stock assessments (e.g. Rivard 1989) but also the most important because it is used to set the next catch quota. Use of fish spotter data in our simulation experiment resulted in an improvement of 26% in the precision of spawning biomass estimates for the last year and may have reduced bias by 17% (i.e. $[12\% - 10\%]/12\%$). These results indicate that indices of relative abundance based

TABLE 5. Sign (+ or -) for ι_2 and its p -value under the null hypothesis that $\iota_2 = 0$ for regression analyses of anchovy abundance indices (equation (9)). Negative estimates indicate saturation. Small p -values (e.g. $p < 0.05$) indicate nonlinearity.

Index	Estimate for ι_2	
	Sign	p -value
T/BAF	-	0.910
Area (A)	-	0.000
Indices from fish spotter data only		
Density for positive blocks (d)	-	0.011
Proportion positive (P)	-	0.000
Relative abundance (I)	-	0.317
Indices from fish spotter and environmental data		
Density for positive blocks (d)	-	0.049
Proportion positive (P)	-	0.793
Relative abundance (I)	+	0.266

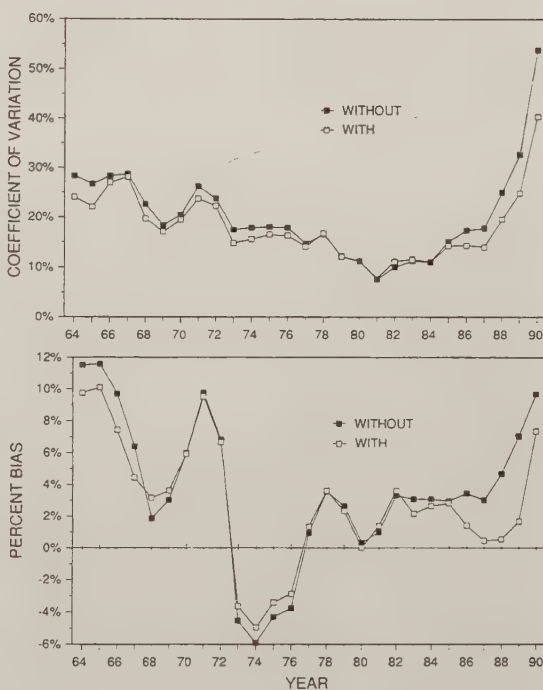


FIG. 5. Coefficients of variation (top panel) and percent bias (bottom panel) for estimates of anchovy total biomass during 1964-90 from the stock synthesis model. Coefficients of variation and percent bias were calculated by simulation for estimates made with and without fish spotter data.

on fish spotter data are cost-effective ways to improve biomass estimates used to manage the fishery for northern anchovy.

Our work extended the delta distribution models proposed by Aitchison and Brown (1957) and Pennington (1983) because both density of anchovy in positive blocks (d) and proportion positive (P) were estimated using models that allowed us to include factors (e.g. pilots) that affected estimates of density and proportion positive and increased the precision of our esti-

mates. Our approach should be applicable whenever the statistical distribution of data is distorted by excessive zeros (e.g. ichthyoplankton surveys) and affected by external factors or covariates, but care should be taken to ensure that the distribution of nonzero data is as assumed for estimation procedures (Meyers and Pepin 1990).

Future Research

The models we developed for fish spotter data may be best suited for relatively short time series because the number of parameters will increase as data are collected for more years and pilots. At some point, the number of parameters may grow large enough to make the models cumbersome and too large for small computers. Future work could usefully be directed towards reducing the number of parameters either by restricting the number of years included in the analysis or developing alternative statistical approaches.

For sufficiently long collections of fish spotter data, it may be possible and advantageous to develop time series models (Abraham and Ledolter 1983). Our approach estimated relative abundance for each year separately and may not have fully utilized the data because relative abundance of fish in adjacent years is usually similar enough to be used for making estimates (Roff 1983).

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Appendix 1. Corrections for Bias and Variance Calculations

Approximate estimates for the variance of relative abundance in each year (I in (8)) were computed by the delta method (Seber 1982):

$$(A1) \quad \text{Var}(\hat{I}) \approx A^2 [\text{Var}(\hat{d}) \hat{P}^2 + \hat{d}^2 \text{Var}(\hat{P}) + 2 \hat{d} \hat{P} \text{Cov}(\hat{d}, \hat{P})]$$

where hats (^) denote estimates, $\text{Var}(\)$ denotes variance, I is the index of relative abundance for anchovy in each year, A is area of the anchovy stock, d is the density of anchovy in positive blocks, P is the proportion positive, and $\text{Cov}(\hat{d}, \hat{P})$ denotes the within-year covariance of estimates for density (d) and proportion positive (P). Variances for estimates of d and P were calculated as described below. The covariance term in (A1) was estimated approximately from the correlation of d and P among years and the within-year standard deviation of d and P :

$$(A2) \quad \text{Cov}(\hat{d}, \hat{P}) \approx \rho_{\hat{d}, \hat{P}} [\text{SE}(\hat{d}) \text{SE}(\hat{P})]$$

where $\rho_{\hat{d}, \hat{P}}$ denotes the correlation and $\text{SE}(\)$ denotes a standard error.

Unbiased estimates of anchovy density in positive blocks (d in (5)) and proportion positive blocks (P in (7)) as well as variance estimates for d and P were calculated as described by Bradu and Mundlak (1970). The correction for bias in (5) and (7) involves a correction factor Ψ (Ψ_d for density and Ψ_p for

proportion positive). Assuming lognormal-distributed errors, the correction factor is

$$(A3) \quad \Psi = g_m \left[\frac{m+1}{2m} (\hat{\xi}^2 - \hat{\xi}_{\eta}^2) \right]$$

where $g_m(\)$ is a function described below, $\hat{\xi}^2$ is the residual variance (σ^2 in (3) for density or δ^2 in (6) for proportion positive), m is degrees of freedom for the estimate of residual variance, $\hat{\eta} = \hat{\beta}_0 + \hat{\beta}_1$ for density (d) or $\hat{\eta} = \hat{\tau}_0 + \hat{\tau}_{1j}$ for proportion positive, and $\hat{\xi}_{\eta}^2$ is the variance of $\hat{\eta}$.

The function $g_m(\)$ in (A3) is

$$(A4) \quad g_m(t) = \sum_{p=0}^{\infty} \left[\frac{m^p (m+2p)}{m(m+2) \dots (m+2p)} \left(\frac{m}{m+1} \right)^p \frac{t^p}{p!} \right]$$

where t is the argument for the function.

Variance estimates for $\hat{d}$ in (5) and $\hat{P}$ in (7) were calculated as

$$(A5) \quad \text{Var}(\cdot) = e^{2\hat{\eta}} \left\{ g_m^2 \left[\frac{m+1}{2m} (\hat{\xi}^2 - \hat{\xi}_{\eta}^2) \right] - g_m \left[\frac{m+1}{m} (\hat{\xi}^2 - 2 \hat{\xi}_{\eta}^2) \right] \right\}$$

where $\text{Var}(\)$ is the variance of either $\hat{d}$ or $\hat{P}$.

Appendix 2. Simulations

First, the stock synthesis model for northern anchovy was modified to include the new index of schooling biomass from fish spotter data. The original stock synthesis model for anchovy included an index of schooling biomass based on a sonar survey conducted by the California Department of Fish and Game during 1969-85 (Mais 1974; Methot 1989). Sonar and fish spotter indices both measure relative schooling biomass, so the pattern of age-specific availability of anchovy to the fish spotter index was assumed to be the same as for the sonar survey (age-specific availability patterns are used in the stock synthesis model to relate the index of schooling biomass to stock age structure). This assumption allowed us to include the new fish spotter index for anchovy with a minimum of additional programming. The fish spotter index was given the same relative weight as other types of information about abundance in the stock synthesis model.

The modified stock synthesis model was fitted to data, including the index based on fish spotter data, for 1964-90. After the model was fitted, predicted values for each type of data were calculated and stored. Standard deviations for the fit of the model to each type of relative abundance data were calculated (assuming a lognormal distribution for discrepancies between observed and predicted values).

Fifty simulated data sets with fish spotter data and 50 simulated data sets without fish spotter data were generated (the number of simulations conducted was limited by available computer time). A pseudorandom number generator, predicted values from the original fit, and standard deviations calculated as described above were used to generate relative abundance data for the simulation experiment. Age composition data were gen-

erated from predicted age compositions by assuming multinomial sampling errors. The stock synthesis model was fit to each of the simulated data sets and coefficients of variation for estimates of spawning biomass during 1964–90 were calculated

to evaluate precision. This approach to estimating coefficients of variation for spawning biomass estimates is a “parametric bootstrap” approach in the language of Efron (1982).

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AGE, LENGTH, WEIGHT, REPRODUCTIVE CYCLE AND FECUNDITY OF THE MONKEYFACE PRICKLEBACK (*CEBIDICHTHYS VIOLACEUS*)

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Life history characteristics of age, length, weight, reproductive season and fecundity of the monkeyface prickleback (*Cebidichthys violaceus*) were investigated. Most specimens were obtained from poke pole anglers during low tides at Dillon Beach, California. Males and females were aged to 18 years old, with males attaining a larger size. Sexual dimorphic growth occurred after age eight, coincident with maturity in females. A complete length-weight curve was constructed. The age-weight curves for males and females were similar. Females mature as early as four years of age with 100% mature by age eight. Spawning occurs from February through April. Two adult females had an estimated 17,000 and 40,000 mature eggs each.

INTRODUCTION

The monkeyface prickleback (*Cebidichthys violaceus*) known to anglers as the monkeyface "eel", are found in rocky intertidal and subtidal habitats ranging from San Quintin Bay, Baja California (Miller and Lea 1972) to Brookings, Oregon (Barton 1978). They are prime targets of the few sports anglers who "poke pole" in the rocky intertidal zone at low tide (Squire and Smith 1977). Little is known about the life history of this species. This paper presents the life history parameters of length, weight, and age of both sexes, as well as some aspects of ovarian maturity, reproductive season and fecundity of females.

METHODS

A total of 401 fish were examined. Of these, 369 were collected 0.5 to 2 km north of Dillon Beach, California, a "semiprotected coastal habitat" (Hedgpeth 1962, Plate

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1); 26 fish from Bodega Bay, California, a "protected coast"; and six fish from Pacifica, California, an "outer, wave swept coast". Fish were taken from the lower intertidal zone (Ricketts and Calvin 1968) during 99 low tide periods of -0.3 to -2.0 feet.

Collecting began in November 1981 and continued intermittently until July 1987. Data on standard (SL) and total (TL) length, weight, and gonads were obtained from fish caught by the first author and/or fishing partners. However, the fishermen scattered along the rocks usually filleted their catch there, so gonads were often not available. Because the first author could not be present at all fishing sites, different numbers of fish were used in the various analyses.

Otoliths (sagittae) were removed, cleaned, and stored dry in gelatin capsules. The small (± 3 mm diameter) otoliths are difficult to extract because the bones of the skull are very thick. The opercle was then evaluated as a structure for aging. The gill covers proved to be easy to dissect with a small wire clipper. Skin and flesh was removed after soaking in a hot solution of a protein-dissolving laundry product (BIZ®). Opercula had very clear growth marks and were stored dry in envelopes. Ages were determined by the second author using a Wild dissecting microscope at 25x and indirect lighting.

Because the otolith is a standard aging structure for marine fishes (Chilton and Beamish 1982), otoliths and opercula from 39 fish were compared to see whether they yielded the same age estimates. The results indicated that they were comparable, and so opercula were used as the standard aging structures. Estimates, using the von Bertalanffy equation of growth parameters, based on both structures from 91 specimens were made. The estimates L_{∞} , k , and t_0 were tested for significance for non-linear models with an F -test after Ratkowsky (1983).

Early in the study, only TL was measured and a conversion to SL was necessary. This was calculated from 177 observations for which both lengths had been measured. The linear regression is:

$$SL = TL (0.931) + 1.416$$

with an R^2 of 0.977.

The age-length data were compiled separately for males and females. Ages determined from opercula were used to estimate parameters of the von Bertalanffy growth model:

$$L_t = L_{\infty} [1 - e^{-kt}]$$

where

L = length at age t ,

L_{∞} = asymptotic length of the species,

k = growth completion rate, and

t_0 = theoretical age at zero length.

Weights were taken for 139 fresh fish ranging from 27 cm and 145 g to 60 cm and 1950 g. Using the equation:

$$W = aL^b$$

where

W = weight in g,

L = standard length in cm for males and females,

Table 1. Comparison of age estimates based on otoliths and opercula of 39 fish.

Age	n	% Agreement	%± 1yr.	%± 2 yrs.
4	2	100		
5	10	50	50	
6	9	55.6	22.2	22.2
7	5	60	40	
8	4		50	50
9	2	50		50
10	2	50		50
13	1		100	
14	2	50		50
16	2			100

resulted in estimates for the constants a and b. Log transformation of the data was performed in order to compare the linear regression statistics.

The number of ovaries obtained each month varied widely, depending on occurrence of low tides (< 0.3 ft) during daylight hours and surf conditions. Also, a major factor was the numbers of fishermen on the rocks during spring and summer months.

Gonads were removed from 196 females and brought to the laboratory to estimate the reproductive stage. Four developmental stages were noted on the basis of their characteristic color using Smithe's (1974) color guide. Immature gonads were pearl grey, maturing gonads contained eggs that were orange yellow or spectrum orange, ripe gonads contained eggs that were chrome orange and resting gonads were flacid and pearl grey.

Gonadal weights and estimates of fecundity of two fish were recorded using a Mettler balance and a dissecting microscope (12x), respectively. Testes from 22 males were collected. Immature testes were threadlike, whereas mature testes were swollen and white, while spent testes were grey-brown and roughly triangular in shape.

RESULTS AND DISCUSSION

The technique for age determination using otoliths is widely accepted and defined (Chilton and Beamish 1982). We followed standard aging techniques where one ring represented one year's growth. We found the otolith to have clear growth rings, but they were very small and were difficult to remove. The opercula were much easier to dissect, had equally clear growth rings, and age determination from the otoliths and opercular were similar. In 30 of 39 comparisons (77%), the two structures had ages either matching or within one year of each other (Table 1).

Growth curves compared from data on 91 fish were not significantly different ($F = 1.0891$, $df = 3,177$) (Table 2; Fig. 1). Estimated size at age was larger for males than females after age eight (Table 3; Fig. 2). Both sexes were aged up to 18 years

Table 2. von Bertalanffy growth model parameter estimates and standard deviations for monkeyface pricklebacks derived from 4 data sets. Comparisons of aging structures using the same data set and for males and females using all ages determined from the operculum.

Structure/Sex	Age (yr)	Length (cm)	L_{∞}	k	t_0	n
Otolith						
Est.	2-18	23-67	72	.10	-1.89	91
S.D.			8	.03	1.08	
Opercle						
Est.	2-18	23-67	71	.10	-2.63	91
S.D.			8	.04	1.31	
Opercle-Females						
Est.	0-18	15-62	62	.14	-1.95	115
S.D.			2	.02	.28	
Opercle-Males						
Est.	0-18	13-67	70	.12	-1.91	74
S.D.			5	.02	.29	

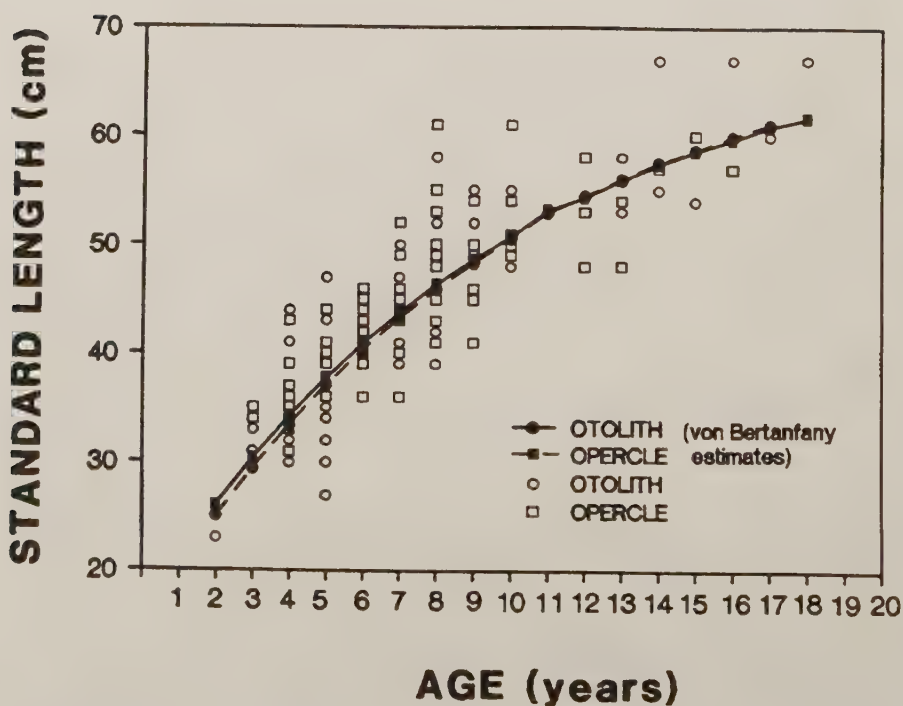


Figure 1. Comparison of growth rates of 91 monkeyface pricklebacks determined from otoliths and opercula.

Table 3. Estimated length at age from the von Bertalanffy growth equation for male and female monkeyface pricklebacks. The size range (CM SL) and numbers sampled of each age group are included.

Age	Males			Females		
	Mean size	Range	<i>n</i>	Mean size	Range	<i>n</i>
0	14	12-16	4	15	14-18	5
1	20	16-25	5	21	18-23	7
2	26	23	1	27	23	1
3	30	33	1	32	31-35	3
4	35	31-44	12	36	32-41	20
5	39	32-36	16	39	27-47	11
6	42	36-44	18	42	36-45	19
7	45	36-50	11	45	41-52	10
8	48	41-58	14	47	39-61	12
9	50	46-55	4	49	41-55	5
10	53	48-61	6	51	50-55	4
11	55	-	0	53	48	1
12	56	53-58	2	54	53-58	2
13	58	48-54	2	55	57-76	3
14	59	55-67	2	56	54-60	2
15	60	-	0	57	-	0
16	61	57-76	2	57	-	0
17	62	60	1	58	-	0
18	-	-		59	67	1
Totals			101			106

with maximum estimated standard lengths of 62 cm for females and 67 cm for males. Estimated length at age is presented in Table 3. Burge and Schultz (1973) presented ages for 12 specimens, which fall into the ranges of ages determined in this study.

Weight data for each sex were compared and the statistics were not significantly different ($P < 0.01$) (Table 4). These data were pooled with weight data on small fish (Edwards 1981) in order to construct a complete weight-length curve (Fig. 3). The 11 weights reported by Burge and Schultz (1973) and the three from Fitch and Lavenberg (1971) fall into the ranges obtained in this study.

Nineteen testes were examined. Eight were from immature males <25 cm, three swollen testes collected in May and June and eight spent testes were collected from May through July.

Fecundity was estimated for two females. One caught 5 February 1982 was seven years old, 41 cm SL, and contained approximately 17,500 mostly mature eggs. A second female caught on 12 March 1982 was 11 years old, 61 cm SL, and contained approximately 46,000 mostly mature eggs.

Examination of ovaries indicated that the sample consisted of 67 immature and 137 mature fish. Age at first maturity was four years (36 cm); 50% were mature at

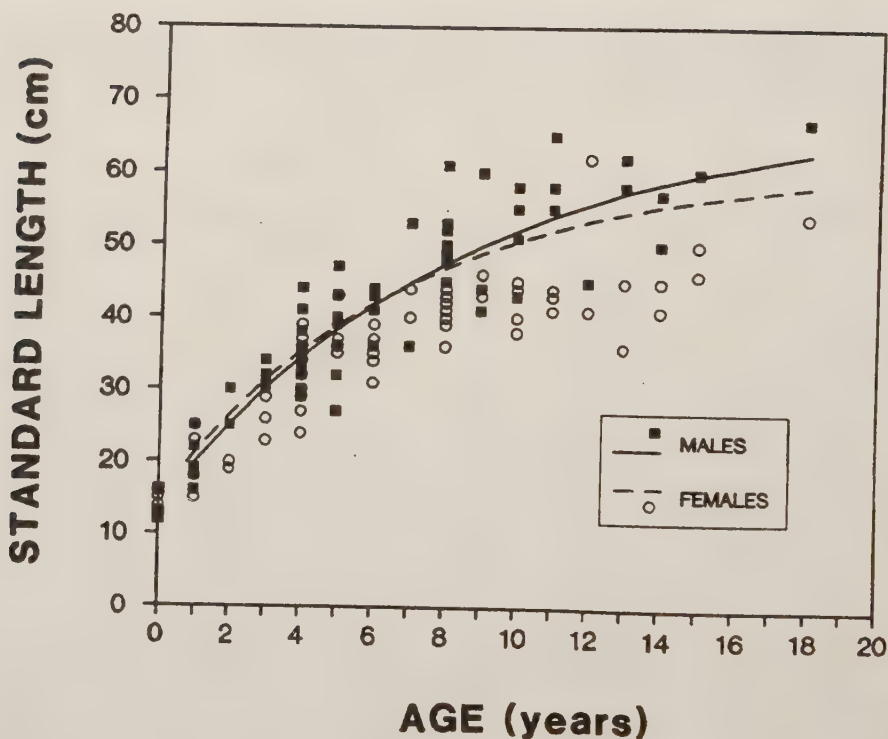


Figure 2. Comparison of growth rates of 171 male and female monkeyface pricklebacks determined from opercula.

Table 4. Weight at length parameters for males, females and for sexes combined from this study, and fish <20 mm from Edwards (1981), where $\text{Weight} = a(\text{Length})^b$. Linear regression statistics for log transformed data where $\ln(\text{Weight}) = a(\ln \text{Length}) + b$. Growth curves for males and females are not significantly different ($P < 0.01$).

$W + aL^b$	a	b	n	r^2
Males	0.006797	3.072	62	
Females	0.0325	2.654	77	
Sexes Combined	0.01289	2.900	139	
This study plus Edwards (1981)	0.00965	2.971	174	
$\ln W = b + a(\ln L)$				
Males	0.0735	3.382	62	0.90334
Females	0.0712	3.393	77	0.85512
Sexes Combined	0.0714	3.399	139	0.87767

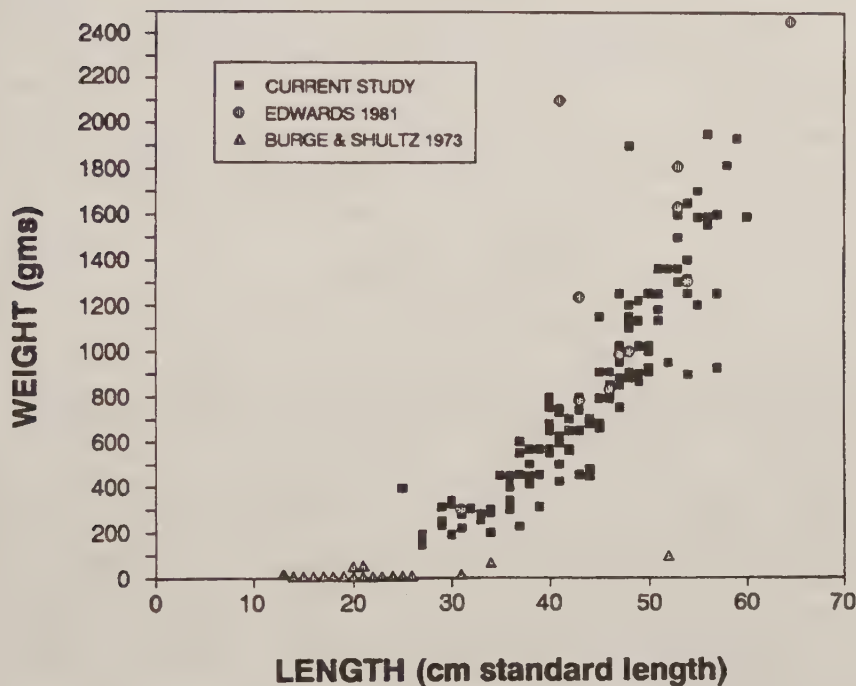


Figure 3. Weight-length relationships from this study and the literature.

five years (39 cm), and 100% were mature at seven years (45 cm). Reproductive activity began in January with the peak months of spawning in February, March and April.

Mature ovaries were collected March-May, maturing ones December-June, and spent ovaries February-August and one in December. The average age of 21 fish with mature ovaries dropped from 11 years (6) to 10 years (7), 8 years (6) and 6 years (2). This indicates that older fish spawned earlier than the younger ones. The small sample of testes indicates a similar pattern.

These data are similar to those reported on the Black Prickleback (*Xiphister atropurpureus*) by Wourms and Evans (1974). They suggest that this species, which also spawns in late winter and spring, are less apt to be exposed to environmental risks of wave shock, reduced salinity and high or low water temperatures.

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Population Genetic Structure of the Armorhead, *Pseudopentaceros wheeleri*, in the North Pacific Ocean: Application of the Polymerase Chain Reaction to Fisheries Problems

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A armorhead (*Pseudopentaceros wheeleri*) occur in the subarctic, epipelagic habitats of the northern Pacific Ocean and are known to reproduce on seamounts in the central Pacific. Over the last few decades, overexploitation of seamount populations led to dramatic declines in abundances of reproductive populations. We undertook a study of the population genetics of armorhead to test whether distinct stocks exist in association with specific seamounts. We used the polymerase chain reaction (PCR) and a combination of DNA sequencing and restriction fragment length polymorphism (RFLP) analysis to analyze mtDNA variants for individuals collected from three localities: two seamounts and from the open ocean. We discovered that mtDNA haplotypes are not partitioned geographically, refuting the hypothesis that different seamounts harbor genetically distinct populations. Furthermore, genetic similarity of seamount and open-ocean fish supports the hypothesis that armorhead migrate between the central and northern Pacific Ocean for reproduction and feeding, respectively.

L'espèce *Pseudopentaceros wheeleri* vit dans les habitats subarctiques épipélagiques de la région septentrionale de l'océan Pacifique et on sait qu'elle se reproduit sur les monts sous-marins de la région centrale de cet océan. Au cours des dernières décennies, la surexploitation des populations des monts sous-marins a conduit à des déclin spectaculaires de l'abondance des populations reproductrices. Nous avons entrepris une étude de la génétique des populations de *P. wheeleri* afin d'examiner s'il existe des stocks distincts en association avec des monts sous-marins particuliers. Nous avons utilisé la réaction en chaîne de la polymérase (RCP) et une combinaison de séquençage d'ADN et d'analyse du polymorphisme de la longueur des fragments de restriction (PLFR) pour analyser les variants d'ADNmt de sujets prélevés en trois endroits : deux monts sous-marins et la haute mer. Nous avons découvert que les haplotypes d'ADNmt ne suivent pas une compartimentation géographique, ce qui réfute l'hypothèse selon laquelle les monts sous-marins différents seraient peuplés par des populations génétiquement distinctes. En outre, la similarité génétique des poissons des monts sous-marins et des poissons de haute mer corrobore l'hypothèse selon laquelle *P. wheeleri* migre entre la région centrale et la région septentrionale de l'océan Pacifique respectivement à des fins d'alimentation et de reproduction.

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The hypothesized life history of armorhead (*Pseudopentaceros wheeleri*) is extraordinary. Eggs and larvae are planktonic. Larvae rapidly develop and assume a nektonic habit. At this stage, juveniles move away from the seamounts and subadult fish are most often observed in the cold, nutrient-rich waters of the North Pacific (Boehlert and Sasaki 1988). After feeding for at least 1-3 yr, individuals are believed to migrate to the seamounts in the central Pacific Ocean, take up a demersal habit, spawn, and die (Humphreys et al. 1989).

A armorhead have been recorded from over a dozen seamounts in the central North Pacific Ocean (Borets 1979; Humphreys

and Tagami 1986). There are often differences in morphology among individual fish captured in the vicinity of a particular seamount as well as among fish captured at different seamounts. Such variation led Hardy (1983) to recognize two distinct species: *P. pectoralis* and *P. wheeleri*. Subsequent work by Humphreys and Tagami (1986) and Humphreys et al. (1989) showed that the morphological variation exhibited by armorhead is associated with the transition from a pelagic to demersal existence coupled with the onset of reproduction. Just after transition from the pelagic stage, individuals have high fat reserves, and ratios of body depth to fork length are usually greater than 0.25. Over time, individuals become leaner as fat reserves are used up, exhibiting body depth to fork length ratios

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of 0.20 and less. Regional differences in morphology among fish are thought to be due to differences in age at recruitment to the demersal stage.

The existence of a single species of armorhead in the North Pacific is supported by allozyme data that show no allele frequency differences between morphologically distinguishable fish from the Hancock Seamount in the Northern Hawaiian Ridge (NHR) (Humphreys et al. 1989). However, Humphreys et al. analyzed fish from only a single seamount, leaving open the possibility that fish at other seamounts, differing in latitude, oceanographic characteristics, size, proximity to other seamounts, and productivity (Uchida et al. 1986), are genetically different.

Elucidation of genetic relationships among the different seamount populations is warranted because armorheads were once (and may again be) commercially important. Furthermore, only the southernmost seamounts (Hancock Seamounts) lie within U.S. waters whereas the remainder are in international waters. If independent gene pools are associated with different physiogeographically distinct seamounts, then efforts to manage the exploitation of these fish can be implemented on a seamount-by-seamount basis. On the other hand, lack of differentiation among fish from different seamounts would suggest that there is a single panmictic population that is widely distributed throughout the North Pacific. In this case, exploitation of these fish anywhere in the North Pacific may impact the entire stock, and management tactics should be implemented accordingly.

We investigated the population genetics of *P. wheeleri* collected from the two seamounts separated by approximately

500 km and from the open ocean (Fig. 1) to determine if there was evidence for genetic differentiation among fish captured near different seamounts. We also determined haplotypes of fish captured in the open ocean and compared them with haplotypes of fish captured near seamounts to provide indirect evidence for migration between sites of reproduction in the central Pacific Ocean and the hypothesized feeding grounds in the North Pacific Ocean. Finally, we compared the haplotypes for morphologically different fishes to test whether there is a relationship between morphological and genetic differentiation and if there is genetic evidence for two species in the North Pacific Ocean. Our approach employed a combination of DNA sequence and restriction fragment length polymorphism (RFLP) analysis of polymerase chain reaction (PCR) amplified gene regions of mitochondrial DNA (mtDNA). These techniques for population genetic analysis of *P. wheeleri* can be applied to other species of interest.

Methods and Materials

Collection of Fish

Demersal adult fish were caught by pelagic longline from two seamounts, Koko and southeast Hancock in the central North Pacific (Fig. 1). Pelagic-phase juveniles were obtained from a region bounded by latitudes 41–44°N and longitudes 157–165°W (Fig. 1) by foreign drift-net vessels. For the fish caught at the seamounts, portions of the liver and oocytes (when present) were initially frozen in liquid nitrogen and then stored at –70°C until analyzed. For the pelagic fish, 1-g samples of

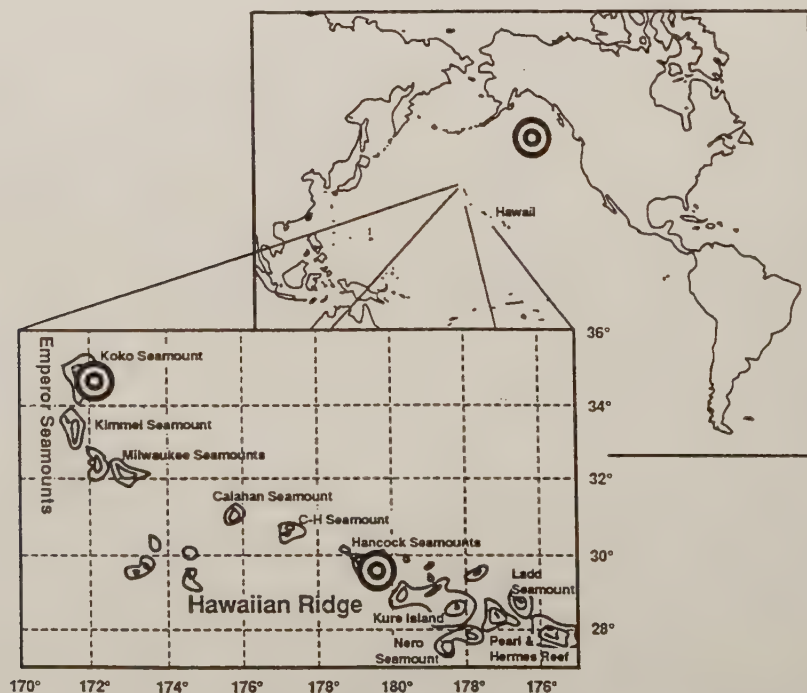


FIG. 1. Map of the Northwestern Hawaiian Islands – Southern Emperor Seamounts showing the location of collection sites for armorheads. Collections were obtained from Koko Seamount, Hancock Seamount, and for pelagic-phase fish from a region bounded by 41–44°N latitude and 157–165°W longitude.

TABLE 1. Primers used for PCR amplification. H and L refer to heavy or light strand, respectively. Numbers correspond to the location of the primer sequence in the human genome sequence (Anderson et al. 1981). Primer sequences are given 5' to 3'. Y = C and T. See Palumbi et al. (1991b) for more information.

Primer	Sequence
Cytochrome oxidase I	
COI-L6569	CCTGCAGGAGGAGGAGAYCC
COI-H7110	CCAGAGATTAGAGGGAATCAGTG
Hypervariable D-loop	
CB3-L15560	CATATTAACCCGAATGATATTT
12SA-H1067	ATAATAGGGTATCTAATCCTAGTTT
Ribosomal genes	
12SA-L1067	AAACTGGGATTAGATACCCCACTAT
16SA-H2492	ATGTTTTTGATAACAGGCG

muscle were placed in homogenization buffer (see below) and stored at 4°C.

Extraction of DNA

Approximately 1 g of tissue was homogenized in 2–3 mL of buffer (250 mM sucrose, 50 mM EDTA, 50 mM Tris, pH 7.5) using a Teflon-glass homogenizer and 1 mL of the homogenate was placed into a 1.5-mL Eppendorf tube. The homogenate was centrifuged for 2 min at 1000g at room temperature. The supernatant was transferred to a new tube and centrifuged at 8000g for 3 min. The resulting pellet was resuspended in 600 µL of fresh buffer and lysed by the addition of sodium dodecyl sulfate (an ionic detergent) to a concentration of 1%. The lysate was extracted once with phenol, once with phenol–chloroform (1:1), and once with chloroform – isoamyl alcohol (24:1). The nucleic acids were precipitated with ethanol and 2.5 M ammonium acetate (pH 7.5), vacuum dried, resuspended in 50 µL of 0.1 × TE, and stored at –20°C. When oocytes were present in individuals, a simpler and quicker method of DNA extraction was substituted. Like most species of teleosts, the oocytes of armorhead are small (<1 mm in diameter). Two to 10 oocytes were suspended in 50 µL of buffer (50 mM KCl, 10 mM Tris, pH 8.3, 1 mM EDTA) and the cells lysed by the addition of NP40 (a nonionic detergent) to a concentration of 1%. The sample was boiled at 95°C for 5 min and sterile distilled water added to a final volume of 100 µL.

Amplification of Mitochondrial Gene Regions

Specific gene regions of the mitochondrial genome were amplified using the PCR (Erich 1989; Palumbi et al. 1991b). Double-stranded DNA was amplified in 50 µL reactions containing 50 mM KCl, 10 mM Tris, 1.5 mM MgCl₂, 0.01% gelatin, 0.01% Triton-X, 0.01% NP40, 1 µM each of oligonucleotide primer, 200 µM each of dNTP, 0.5 unit of Taq polymerase, and 1 µL of the DNA sample. Thermal cycling parameters were as follows: denaturation at 94°C for 40 s, annealing at 55°C for 25 s, and elongation at 72°C for 1–2 min. For the purpose of sequencing, single-stranded templates were generated by adding 1 µL of the double-stranded reaction to a 100-µL reaction containing only a single primer and all of the amplification reagents. The same conditions for single-stranded amplification were used as in double-stranded amplifications. Primers were synthesized on a Biosystems PCR Mate Oligonucleotide Synthesizer.

We routinely amplified three distinct gene regions of the mitochondrial genome of *P. wheeleri*: a 450-bp region of the cytochrome oxidase I gene, a 1425-bp region comprising most

of the 12S rRNA gene and the 5' half of the 16S rRNA gene, and an approximately 2000-bp fragment containing the entire D-loop including flanking gene regions on both sides. Primer sequences are given in Table 1.

DNA Sequencing

Single-stranded templates were purified by centrifugal ultrafiltration through Centricon 30 tubes. DNA sequencing of the cytochrome oxidase fragment was performed using the Sequenase system (USBiochemicals). Fragments were separated through 6% acrylamide, 7 M urea buffer – gradient gels (Palumbi et al. 1991b) and the radioactive bands from the sequencing reaction were visualized by exposure to X-ray film for 24–48 h (Fig. 2).

Endonuclease Restriction Analysis

The ribosomal genes and D-loop region were amplified as described and 12 µL of the amplified sample subjected to endonuclease digestion using the four-base recognition enzymes *Hae* III, *Mbo* I, and *Msp* I. Digestions were performed directly in the PCR buffer at 37°C for 4–6 h. The DNA fragments were separated in 1–1.5% agarose gels, stained with ethidium bromide, and the fragments made fluorescent by exposure to ultraviolet light and photographed (Fig. 3). The presence or absence of restriction sites was inferred from comparisons of fragment patterns (Palumbi et al. 1991a), and composite genotypes were assigned to each individual.

Genetic Relationship among Genotypes

The topology of relationships among genotypes was determined using the principle of parsimony (PAUP, Swofford 1989), treating the restriction site changes as Dollo character types. Restriction sites in the ribosomal and D-loop fragment were assigned weights of 5 and 1, respectively, reflecting the fact that ribosomal genes evolve considerably slower than the D-loop (Cann et al. 1987). Equal weights were also considered. We tested for differentiation among the seamount and open-ocean fish by standard contingency analysis and the G_{ST} test of Takahata and Palumbi (1985). Significance levels were determined using randomization tests (Roff and Bentzen 1989; Palumbi and Wilson 1990). In addition, average nucleotide diversity was estimated following Takahata and Palumbi (1985). The estimation of migration rate, Nm , was done using the method of Slatkin and Maddison (1989) based on the inferred topology of the relationships among distinct alleles.

Results

DNA Sequence Analysis

DNA sequences were determined for a 353-bp region of the cytochrome oxidase I gene for 10 individuals from each of the two seamounts (Fig. 2). Only a single C–T transition nucleotide substitution at a silent site (third “wobble” position of a codon) was found that distinguishes two mtDNA genotypes. This sequence variant was observed in four individuals: three from Koko and one from southeast Hancock Seamounts, respectively. None of the pelagic fish were sequenced. Based on all pairwise sequence comparisons for this gene region, the average (± 1 SD) nucleotide diversity of $0.10 \pm 0.14\%$. However, because most of the nucleotide positions (approximately two thirds) of the cytochrome oxidase I gene are invariable due to selective constraints on the protein, a more

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CTT GGC TAC ATA GGC ATA GTG TGA GCT ATA ATA GCA ATC GGC CTC CTA
T.. ..A ... ..T ..G ..C ... ..G ... T.. ..T ... T.. ...

GGG TTT ATT GTC TGG GCC CAC CAC ATG TTC ACA GTG GGA ATA GAC GTA
... ..C ..G ..A ..A ... ..T ..A ..T ... ..A ... ..T ...

GAC ACC CGT GCC TAC TTC ACG TCC GCC ACT ATA ATT ATC GCA ATT CCC
... ..A ..A ..A ..T ... ..C ... ..T ..C ... ..C ... ..T ..C ...

ACC GGT GTT AAA GTT TTC AGC TGA CTC GCC ACC CTC CAT GGG GGA AAC
... ..C ..C ... ..A ..T ... ..A ... ..C ..A A.C ...T

ATC AAA TGA GAC ACA CCA CTT CTA TGA GCC CTA GGC TTT ATC TTC CTC
..G ... ..TCT G.T G.. G.G ..C ... ..A ..C ... ..T ..T

TTT ACA GTA GGG GGC TTA ACA GGG ATT ATC CTT GCC AAY TCT TCT TTA
..C ..C ... ..T ... C.G ..T ..C ... G.A T.A ..A ..C ..A ..A C..

GAC ATT GTG CTC CAT GAC ACA TAC TAT GTA GTA GCC CAC TTC CAC TAC
... ..C ..A ..A ..C ... ..G ... ..C ..T ... ..C ... ..T ..T

GTA CTA TCA ATA GGA GC
..C ... ..C ... ..C ...

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FIG. 2. A 353-bp DNA sequence for a region of the cytochrome oxidase I gene from armorhead (above) aligned with the homologous region from human (below). The only variable nucleotide position detected from analysis of 20 individuals is a C-T transition mutation represented as a Y in the armorhead sequence and marked by an asterisk. The human cytochrome oxidase I sequence begins at position 6705 in the published sequence (Anderson et al. 1981).

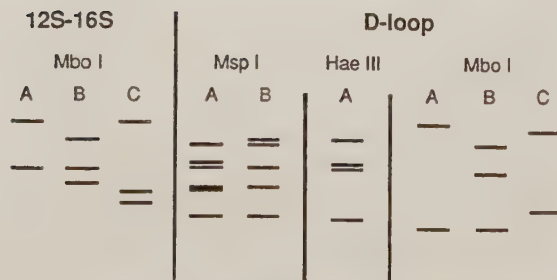


FIG. 3. Fragment pattern profiles for endonuclease digestions of the 12S-16S ribosomal gene regions and the D-loop.

informative estimate is the average percent sequence divergence at silent, third codon ("wobble") positions. Based on these data, this value is $0.30 \pm 0.42\%$.

Endonuclease Restriction Site Analysis

A 1425-bp fragment containing large portions of the 12S and 16S rRNA genes as well as the lysine transfer RNA was amplified for all individuals. Although this region is conserved in all metazoans examined to date, there are short variable regions that are useful for describing intraspecific relatedness. Digestion of this fragment with *Mbo* I detected three different fragment patterns inferred to be the result of polymorphisms at two restriction sites (Fig. 3). Digestion profiles for *Hae* III and

TABLE 2. Comparison of estimates of nucleotide diversity based on direct DNA sequence analysis and indirect restriction site analysis. *D* is the average percent nucleotide diversity. Length represents the approximate amount of the mtDNA genome (in base pairs) represented by the gene region. *N* is the average number of nucleotide differences between two individuals estimated as $(D \times \text{length})/100$. *S* = sequencing and *R* = restriction site analysis.

Gene region	<i>D</i>	Length	<i>N</i>	Method
Protein coding	0.10	12 000	12	S
Ribosomal	0.64	2 700	17.3	R
D-loop	1.87	1 000	18.7	R
Total		≈ 16 000	48	

Msp I revealed four and one restriction sites, respectively, that were monomorphic for 17 of the individuals analyzed by sequencing and thus were not used for the remainder of the samples. (Three individuals that were sequenced were omitted from restriction site analysis because PCR amplification and subsequent endonuclease digestions yielded uninterpretable results.) For the 17 individuals surveyed with three 4-bp recognition enzymes, nucleotide diversity in the ribosomal fragment was estimated as 0.64%.

We also developed primers that routinely amplify an approximately 2000-bp fragment containing the entire D-loop and adjacent flanking regions. We focused on this region because most intraspecific mtDNA nucleotide variation occurs in this region (Cann et al. 1987). The hypervariability of the D-loop is thought to be due in part to frequent length mutations and lack of constraint on sequence change (Saccone et al. 1987).

Initial screening of this region with *Hae* III, *Mbo* I, and *Msp* I for the same 17 individuals analyzed for ribosomal gene variation and cytochrome oxidase I sequences showed an average nucleotide diversity for this region of 1.87%, greater than 10 times the amount of variation detected by sequencing a small portion of the cytochrome oxidase I gene (Table 2).

Population Differences

For both ribosomal and D-loop regions, an additional 67 individuals were surveyed using restriction digestion analysis. A total of 10 distinct mtDNA types were detected. PAUP analysis yielded two most parsimonious trees depicting the relationships among the mitochondrial haplotypes. We used the strict consensus option in PAUP to construct a topology which summarizes the information contained in the two most parsimonious trees (Fig. 4).

The most common type (designated A) was identified in over 64% of the fish surveyed. The frequency of occurrence of the next most common type was only 9.2%. The remaining types were rare, with frequencies of occurrence of 5% or less. Based on the restriction site data for all individuals combined, the overall average percent sequence diversity in the ribosomal and D-loop regions was 1.2%.

No significant differences in allele frequency were detected among the three populations surveyed (chi-square = 14.4, df = 16, $p > 0.5$). G_{ST} analysis revealed that 6.7% of the genetic variation is distributed among groups. Bootstrap analysis indicates that this level of partitioning of genetic variation is not significantly different from random ($p > 0.25$). Using the approach of Slatkin and Maddison (1989), we estimated that, on average, greater than 10 mitochondrial haplotypes have been exchanged among the three populations (Koko, southeast Hancock, and pelagic phase) per generation ($Nm > 10$). (This result also holds for the topology generated from unweighted data.) Theory suggests that for Nm values greater than unity,

there is sufficient gene flow among populations to inhibit genetic differentiation by drift. Thus, the genetic data do not provide evidence for significant population structure of armorhead in the North Pacific.

The individual fish sampled from the two seamounts were identified as being either lean, intermediate, or fat types according to the ratio of fork length to body depth categories defined by Humphreys et al. (1989). A contingency test showed no significant genetic differentiation among the three morphological classes (chi-square = 18.3, df = 20, $p = 0.57$).

Discussion

Variability of mtDNA in Armorhead

The cytochrome oxidase I sequence data indicated a low level of intraspecific nucleotide variability in this species. Only a single variable position was observed in 7020-bp surveyed (20 individuals $\times$ 351-bp). To our knowledge, this is the lowest level of mtDNA nucleotide variability documented for a vertebrate species using these techniques. By contrast, there is appreciable levels of nuclear gene diversity (average heterozygosity = 0.077 (Humphreys et al. 1989)). If the low level of mtDNA diversity is a real phenomenon, then this discrepancy in estimates of genetic variation may indicate that populations of these fish underwent a transient bottleneck event, perhaps relatively recently (Wilson et al. 1985).

It is important to point out, however, that at this time we are unable to directly compare the estimate of nucleotide diversity in armorhead with other taxa because we sampled only a small section of a single gene whereas most other studies of mtDNA variability have employed RFLP analysis of whole mtDNAs (e.g. Graves et al. 1984; Avise et al. 1987). Although we surveyed 117 silent sites (the third "wobble" positions of codons), this amount of sequence is insufficient for reliable estimation of genetic divergence between mtDNAs (Martin

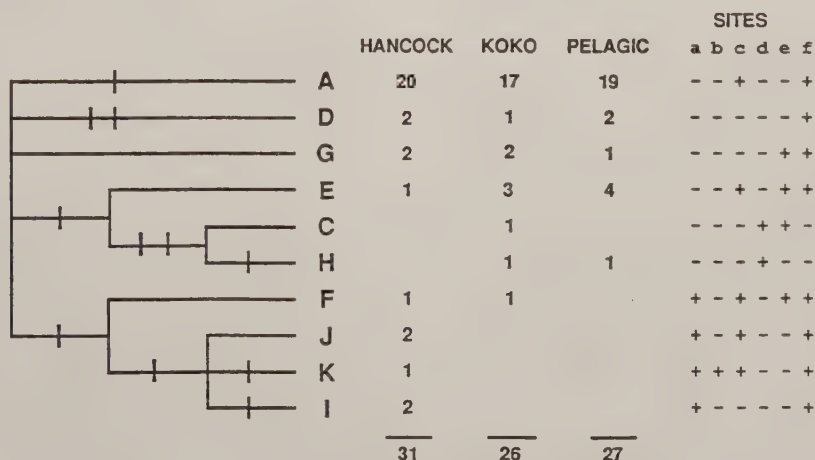


FIG. 4. Inferred topology of the relationships among the 10 mtDNA types identified by endonuclease restriction analysis. Individual tick marks represent site gains or losses. Sites are presented as gains (+) or losses (-) of restriction sites based on the fragment patterns in Fig. 3. Numbers of individuals possessing a particular mtDNA types are given. Site designations are as follows (see Fig. 3 for reference): a, 12S-16S *Mbo* I site gain from A to B; b, 12S-16S *Mbo* I site gain from A to C; c, D-loop *Msp* I site loss from A to B; d, D-loop *Mbo* I site gain from A to C; e, D-loop *Mbo* I site loss from B to A; f, D-loop *Mbo* I site loss from A to C. Consistency index, excluding uninformative sites, is 0.70.

et al. 1990). Thus, the low level of mtDNA sequence variability detected may be a real phenomenon or reflect the limited number of base pairs sampled; therefore, the transient bottleneck hypothesis is highly speculative.

Population Structure

The mtDNA data indicated lack of differentiation between fish collected at different seamounts and from the open ocean. These data provide support for the hypothesized life history and suggest that individuals born at the southernmost seamounts, for example, are equally as likely to reproduce at northern seamounts as at southern seamounts in the next generation. However, we detected few genetic markers that afforded limited resolution of within-species genealogy making it possible that further analysis of armorhead may reveal significant genetic differentiation among fish collected near different seamounts.

One or Two Species?

Based on analysis of the cytochrome oxidase I sequence data and restriction digestion profiles, there is no evidence for genetic differentiation between the three morphotypes of armorhead, identified as lean, intermediate, and fat using the ratio of body depth to mean fork length (Humphreys et al. 1989). In addition to analyses of morphology and allozyme variation, the lack of mtDNA differentiation between morphotypes provides convincing evidence for the existence of only a single species of North Pacific armorhead.

D-loop Amplification for Rapid Genetic Analysis of Fish Populations

DNA sequence analysis provides high-resolution data for population genetic studies because individual nucleotide substitutions can be identified. Unfortunately, DNA sequencing is more expensive and time consuming than indirect but lower resolution methods like restriction site analysis. We find that restriction site analysis of amplified D-loop fragments allowed detection of more nucleotide variation than direct sequence analysis of a 353-bp region of the cytochrome oxidase I gene (Table 2). Although DNA sequence data of D-loops provide superior resolution of genetic relationships among individuals (Meyer et al. 1990; di Rienzo and Wilson 1991), it is possible to distinguish mtDNA types using our technique of PCR amplification of the hypervariable D-loop and endonuclease restriction analysis. This method is rapid, does not require freezing tissue samples to -70°C , and does not involve radioactivity for visualization of DNA, enabling analysis of large numbers of individuals for only a fraction of what sequencing would cost. In addition, variant genotypes identified by restriction digestion can be sequenced directly from the amplification reaction (Palumbi et al. 1991b) in order to ascertain exact sequence divergence.

Acknowledgements

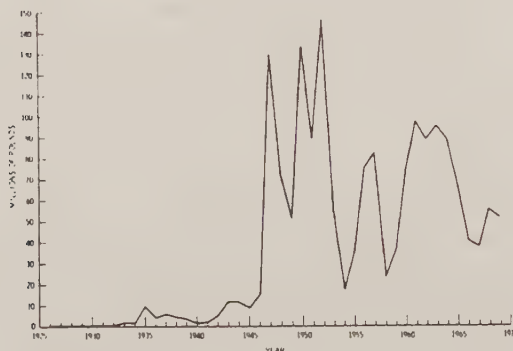
This work was supported by National Science Foundation grants to S.R.P. and by the National Marine Fisheries Service, NOAA. We thank W. O. MacMillan and J. Brown for assistance in the laboratory.

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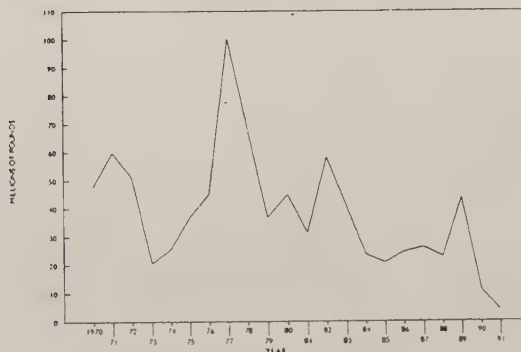
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name jack mackerel for use on all labeling in 1948. This name had more consumer appeal than horse mackerel, and jack mackerel has been a major contributor to California's commercial landings ever since.

Over 90 percent of the jack mackerel landed have been caught in southern California waters by purse seine and lampara vessels. Sporadic catches also occur off Monterey, to the north, as well as Ensenada, Mexico. Jack mackerel are fished throughout the year by the southern California fleet, nearshore from Point Conception to San Diego and offshore as far as San Nicholas Island and Tanner and Cortez banks.



California commercial landings of jack mackerel, 1926-1969.



Commercial landings of jack mackerel, 1970-1991.

JACK MACKEREL

History of the Fishery

The jack mackerel (*Trachurus symmetricus*) was reported in the commercial catch as early as 1888, but was of minor importance before 1947. Commercially, it was less significant than the better known, more profitable, and more abundant Pacific sardine and the more desirable Pacific mackerel. Much of the catch between 1926 and 1946 was taken in schools mixed with sardine and Pacific mackerel and was sold at fresh fish markets where it did not spoil as quickly as Pacific mackerel. Landings were low, varying between 200 and 15,000 tons. During those years it was referred to as "horse mackerel" and had relatively little appeal as a canned product. During the 1947-48 season, the canning industry, after being hit hard by poor sardine landings, turned to jack mackerel as a substitute for sardines and the fishery landed approximately 71,000 tons. The U.S. Food and Drug Administration authorized the common

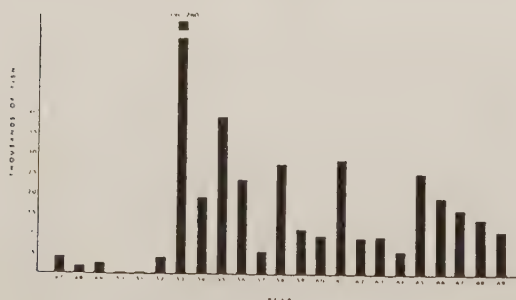
In the early days of the fishery, shortly after 1947, the monthly catches were closely related to the activity of the fleet searching for sardines and Pacific mackerel. Fleet activity was most intense in the fall, when fishermen were searching for sardines, and slowest during the spring, when the sardine season closed and Pacific mackerel were scarce. Landings were highest in the fall and lowest in spring and summer. This seasonal trend soon disappeared when jack mackerel were found to be available throughout the year. In the 1970's landings were slightly higher in the summer when the anchovy fishery was closed and anchovy fishermen sought jack mackerel.

Jack mackerel landings have fluctuated widely. Many of these fluctuations were related to changing market demand and

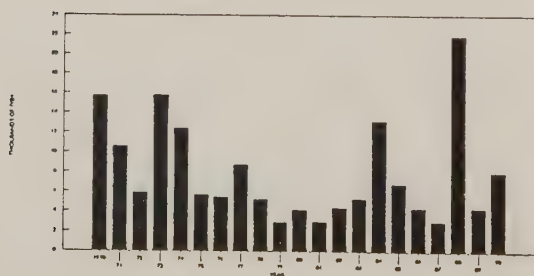
the ability of the fleet to fish for other species which were more profitable or more available. More fishing effort was directed toward jack mackerel when alternative species were unavailable. This happened with the decline of Pacific sardines in 1947 and of Pacific mackerel in 1966. When the Pacific mackerel population started to recover in 1978, the focus of the purse seine fleet's effort soon shifted back to that species, and jack mackerel became a secondary target.

The availability of jack mackerel also plays a part in the erratic catches, since there are unpredictable times when seiners cannot find jack mackerel schools for several months. Purse seiners can catch jack mackerel only when the young fish, less than six years old, form schools near the surface. As jack mackerel grow older, their behavior changes and they inhabit deeper waters farther offshore. There is currently no directed fishery for these older jack mackerel, but they are caught incidentally from California to Alaska, nearshore by salmon trollers, bottom and midwater trawlers, and offshore by albacore trollers.

In the first decade of the southern California fishery, the catch was mostly fish of age three to age six. Since 1965 the catch has been primarily fish of age zero, one, and two; fish older than age two have composed less than 20 percent of the catch. The reasons for the change in the age composition of the catch are not known. Because the purse seine fleet catches primarily age zeros, ones, and twos, the fishery depends on just three seasons' spawning production. If three seasons occur together which produce few young fish there will be very few jack mackerel available to the fishery.

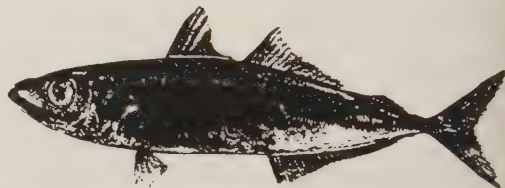


California commercial passenger-carrying fishing vessel (CPFV) landings of jack mackerel, 1947-1969.



California commercial passenger-carrying fishing vessel (CPFV) landings of jack mackerel, 1970-1990.

Large jack mackerel have occasionally contributed to the partyboat sport fishery. In 1953, a run of large fish was encountered in southern California which contributed 13 percent of the partyboat catch in southern California and 8.6 percent statewide. That was an exceptional year and, since then, jack mackerel have been of minor importance to the party boat fleet. Smaller jack mackerel are caught at times from fishing piers in southern and central California.



Jack mackerel, *Trachurus symmetricus*.

Status of Biological Knowledge

Jack mackerel are actually members of the jack family, Carangidae, and are not true mackerel. There are two different behavior patterns during their life. Small fish are found over shallow rocky reefs, generally less than 200 feet deep, and along rocky shorelines of the coast and islands off southern California and Baja California. Large fish, more than 16 inches in length, are found offshore and farther north; they do not form the dense, shallow water schools observed in young fish, but are either solitary or in loose aggregations. The older jack mackerel extend to the Gulf of Alaska and as far west as 162° W longitude. Their movement into the Gulf of Alaska appears to be related to summer warming of the surface waters. Not all the larger fish migrate north, since some large jack mackerel are caught off southern and Baja California waters throughout the year.

Like anchovy and Pacific mackerel, jack mackerel appear to be multiple spawners, but it is not known how frequently a female spawns during a season. Most (70%) female jack mackerel from the southern California fishery become mature near or just after their first birthday in July. By their second birthday, 90 percent of the females are spawning. Very young spawners produce fewer eggs and reach reproductive condition later in the season than do older spawners. Most of the eggs are spawned in 57° to 61° F water. Eggs are about .04 inch in diameter and float free in the ocean for three to five days before hatching, depending on the water temperature.

Jack mackerel spawn offshore from Punta Eugenia to Point Conception from March through August. Their eggs and larvae are uncommon within eighty miles of shore, and often are found as far as 400 miles offshore. This indicates the important contribution of eggs from the large offshore fish. Spawning extends to northern California waters and closer to shore in the Southern California Bight from July through September. Larvae have been taken 100 to 1,000 miles off Oregon and Washington in August and October; they feed primarily on copepods. Juvenile jack mackerel appear to move inshore to concentrate over shallow rocky reefs in the southern California

Bight and along the Baja California coast, for few young fish are found elsewhere.

Young jack mackerel seem to prefer copepods, pteropods, and euphausiids, although at times they feed almost exclusively on juvenile squid and anchovies. Food habits of the older offshore fish are unknown. Jack mackerel, in turn, may be quite important food for billfish. They also contribute to the diet of seals, sea lions, some porpoises, yellowtail, white seabass, bonito, bluefin tuna, striped marlin, angel, and blue sharks.

Status of Population

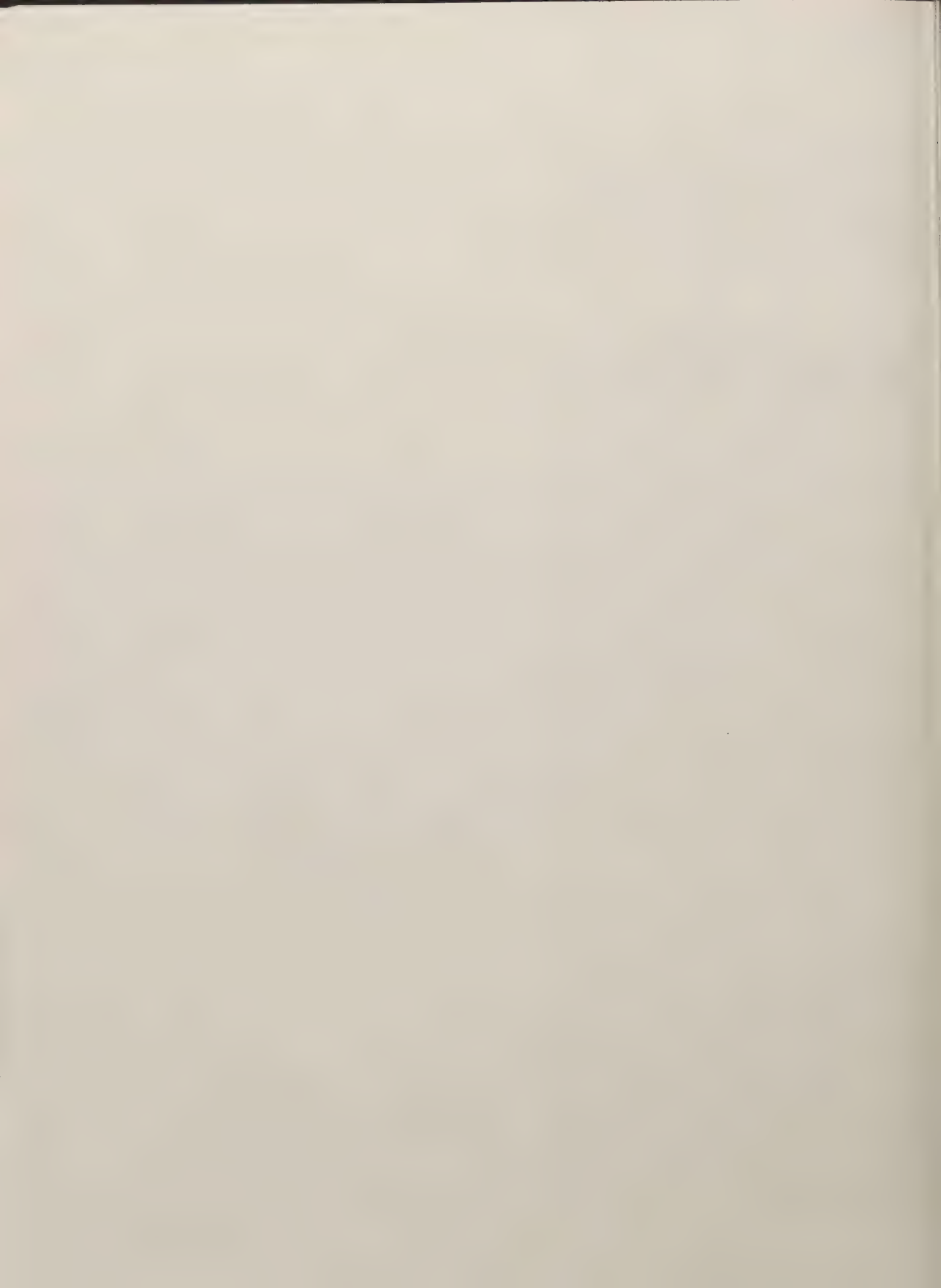
The most recent estimate of biomass was made in 1983. Spawning biomass was estimated at 1.50, and total biomass at 1.63 to 1.99 million tons. These estimates must be viewed as tentative approximations of the population because of two factors. First, the spawning frequency of jack mackerel is not yet known, and so estimates were based on the spawning frequencies of other pelagic species. Second, estimates were derived from CalCOFI egg and larval surveys which did not cover the entire range of the spawning population, so assumptions were made for the contribution of older jack mackerel outside the CalCOFI area. The occurrence of only young fish in the fishery leaves the age structure of the rest of the population unknown, and it is uncertain how much the reproduction of these older fish contributes to the population of young fish in the Southern California Bight.

There has been a decrease in the percent of older fish in the catch since the 1960's, which has caused some concern. It is unclear whether this change is due to a decrease in the number of older fish or to a change in the distribution of the three to six year old fish. The population can probably continue to support the current level of fishing exploitation from the purse seine fleet, but it is difficult to predict the effects of increased exploitation, due to the limited knowledge of the composition and behavior of the older segment of the population and to the limited knowledge of reproduction and recruitment in jack mackerel.

Jan Mason
National Marine Fisheries Service

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Capillary-fiber geometrical relationships in tuna red muscle

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The aim of this study was to examine the size and geometry of the capillary network in tuna red muscle, one of the most aerobic muscles in fish. Deep red muscle of 1.5- to 2-kg skipjack tuna, *Katsuwonus pelamis*, was perfused fixed *in situ*, processed for electron microscopy, and analyzed by morphometry. Fiber cross-sectional area was 560 ± 30 (SE) μm^2 in the samples. Capillary length per fiber volume was 4143 ± 242 (SE) mm^{-2} and mitochondrial volume density 28.5 ± 1.0 (SE) %. Indexes of capillarity such as average number of capillaries around a fiber, capillary length and surface per fiber volume, and capillary surface per fiber surface were high for a fish muscle. In fact, the size of the capillary-fiber interface (i.e., capillary to fiber surface) at a given mitochondrial volume per fiber was not significantly different in tuna red muscle compared with rat soleus muscle. However, calculation of mitochondrial respiratory rates in tuna red muscle yielded a substantially lower value (approximately 1/20th) compared with muscles of mammals. Besides the possible effect of differences in operating temperatures and (or) mitochondrial function(s) in fish compared with mammals, this suggests that the large capillary-fiber interface in tuna may be related to functions other than oxygen delivery per se, such as substrate and (or) heat transfer between capillaries and muscle fiber.

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Le but de cette étude était de déterminer la taille et la géométrie du réseau de capillaires dans le muscle rouge du thon, l'un des muscles les plus aérobiques rencontrés chez un poisson. Des muscles rouges profonds de Thons à ventre rayé, *Katsuwonus pelamis*, de 1,5 à 2 kg ont été fixés par perfusion *in situ*, préparés pour examen au microscope électronique et analysés par morphométrie. La surface d'une coupe transversale de fibre était de 560 ± 30 (erreur standard) μm^2 dans les échantillons. La longueur de capillaire par volume de fibres a été évaluée à 4143 ± 242 (erreur standard) mm^{-2} et la densité volumique mitochondriale, à $28,5 \pm 1,0$ (erreur standard) %. Les indices de la capillarité, notamment le nombre moyen de capillaires autour d'une fibre, la longueur et la surface de capillaire par volume de fibre et la surface de capillaire par surface de fibre étaient élevés pour un muscle de poisson. En fait, la taille de l'interface capillaire-fibre (i.e., surface capillaire par rapport à celle des fibres) pour un volume donné de mitochondries par fibre dans le muscle rouge de thon était semblable à celle du muscle soleus de rat. Cependant, le calcul des taux respiratoires mitochondriaux dans le muscle rouge du thon a donné des valeurs beaucoup plus faibles (environ 1/20) que celles obtenues dans des muscles de mammifères. En plus des effets dus aux différences de températures ambiantes ou bien de fonctionnement des mitochondries entre les poissons et les mammifères, il est possible que l'importante interface capillaire-fibre chez le thon soit reliée à des fonctions autres que celle du transport d'oxygène per se, par exemple le transfert de substrat ou bien de chaleur des capillaires aux fibres musculaires.

[Traduit par la rédaction]

Introduction

With more and more attention being devoted to the capillary-muscle fiber interface, understanding the three-dimensional arrangement of capillary networks has taken on new importance in probing blood-tissue exchange kinetics. Most current quantitative studies of capillary geometry have focussed on mammalian and avian muscles (Mathieu-Costello *et al.* 1988; Mathieu-Costello 1991a, 1991b). They led to the following generalizations: (i) the use of capillary number per sectional area of fibers in transverse sections only ('capillary density') can underestimate capillary length by as much as 50-70% in shortened muscles; capillarity estimates must take into account the three-dimensional arrangement of the capillary network; (ii) capillary tortuosity within a spectrum of mammalian species (large to small) is a function of sarcomere length, not aerobic capacity; (iii) however, there was less tor-

tuosity and a smaller effect of fiber shortening in the pectoralis muscle of the pigeon than in mammalian muscles; and finally (iv) in pigeon flight muscle, venular portions of the capillaries were arranged perpendicularly to muscle fibers, forming capillary manifolds around groups of fibers (Potter *et al.* 1991). Besides facilitating gas exchange and increasing O_2 extraction at the venular end of the network, the capillary manifolds could be involved in other functions such as heat transfer, and (or) the suggested blood-pumping action of the muscle during flight.

To gain further insight into the geometry of blood-tissue exchange in relation to mitochondrial metabolic capacity, the data base was extended to the flight muscles of bat and hummingbird (Mathieu-Costello *et al.* 1992a, 1992b). The main difference between bat and hummingbird flight muscles was the lack of capillary manifolds in the former and a lesser tor-

TABLE 1. Sarcomere length, l_0 , mean fiber cross-sectional area ($\bar{a}(f)$), capillary number per fiber cross-sectional area ($Q_A(0)$), and capillary diameter ($\bar{d}(c)$) in skipjack tuna muscle

Animal No.	Muscle No.	Site No.	l_0 (μm)	$\bar{a}(f)$ (μm^2)	$Q_A(0)$ mm^{-2}	$\bar{d}(c)$ (μm)
Red muscle						
1	1	1	1.78 $\pm$ 0.01	570 $\pm$ 40	3055 $\pm$ 147	3.79 $\pm$ 0.05
1	2	2	1.74 $\pm$ 0.01	644 $\pm$ 32	2686 $\pm$ 161	3.56 $\pm$ 0.04
2	3	1	1.87 $\pm$ 0.01	578 $\pm$ 20	2513 $\pm$ 72	5.11 $\pm$ 0.04
2	4	3	1.77 $\pm$ 0.01	709 $\pm$ 28	2421 $\pm$ 79	5.39 $\pm$ 0.06
3	5	1	1.77 $\pm$ 0.01	465 $\pm$ 8	3712 $\pm$ 112	3.87 $\pm$ 0.04
3	6	4	1.85 $\pm$ 0.02	458 $\pm$ 26	3476 $\pm$ 176	3.56 $\pm$ 0.04
4	7	5	1.72 $\pm$ 0.02	542 $\pm$ 20	2653 $\pm$ 119	3.35 $\pm$ 0.04
4	8	2	1.77 $\pm$ 0.02	513 $\pm$ 12	2524 $\pm$ 94	3.47 $\pm$ 0.04
$\bar{x}(n = 8)$			1.78 $\pm$ 0.02	560 $\pm$ 30	2880 $\pm$ 171	4.01 $\pm$ 0.28
White muscle						
2	9	6	1.83 $\pm$ 0.01	4191 $\pm$ 168	543 $\pm$ 31	3.60 $\pm$ 0.11

NOTE: Values are given as means $\pm$ SE. For sample site identification, see Fig. 1.

tusosity in the latter. In addition, compared with skeletal and cardiac muscle in other mammalian species, both muscle types displayed twice the capillary length density (capillary length per fiber volume at a given mitochondrial volume density). Similarly, capillary surface per fiber surface at a given mitochondrial volume per fiber was also some 2 times larger than in other mammalian muscles. These observations are consistent with the suggestion of an important functional role for the capillary-fiber interface in blood-tissue O_2 fluxes (Honig *et al.* 1991), and with measurements of O_2 uptake per millilitre of mitochondria in flying hummingbirds that are about twice as high as those in locomotory muscles of mammals running at $\dot{V}\text{O}_{2\text{MAX}}$ (Suarez *et al.* 1991).

The purpose of this study was to further investigate capillary-fiber geometry in highly aerobic fish muscle and to compare the results with the above findings in mammalian and avian muscles. Tuna were chosen because they are capable of high swimming velocities and metabolic rates. Fish red cells are nucleated (as in bird) and can be larger than bird red cells (Altman and Dittmer 1961; Schmidt-Nielsen 1984). One might therefore anticipate both similarities and differences in rheological constraints on O_2 delivery to the muscle fibers in fish and bird muscle compared with mammalian muscle. In this study, we specifically addressed the question of whether or not the tuna red muscle (i) shows a similar capillary arrangement to that of pigeon, bat pectoralis muscle, or other mammalian muscles; (ii) has as high a capillary length density per volume density of mitochondria as that of bat and hummingbird muscles; and (iii) has as high a capillary surface per fiber surface, at a given mitochondrial volume per fiber, as that of bat and hummingbird flight muscles.

Materials and methods

Five skipjack tuna (*Katsuwonus pelamis*; body mass, M_b , 1.5–2 kg; fork length, 43–44 cm) of undetermined sex were used in this study. They were purchased from local commercial fishermen and held for up to 4 days in outdoor 10-m diameter tanks supplied with continuously flowing seawater ($25 \pm 1^\circ\text{C}$) at the Kewalo Research Facility, National Marine Fisheries Service, Honolulu, Hawaii. After being netted and anesthetized with sodium pentobarbital (40 mg/kg i.p.), they were suspended ventral side up at the surface of a small aquarium. The gills were irrigated with seawater during the entire

procedure. A midline incision was made to expose the heart. Heparin (2000 U) was injected directly into the ventricle, followed by papaverine hydrochloride (30 mg). A cannula was inserted into the ventral aorta through the bulbus arteriosus, and the sinus venosus was cut open to secure outflow. Vascular perfusion fixation of the muscles was performed in four animals and infusion of casting material in one animal.

Muscle fixation by vascular perfusion

We followed the same procedure as described elsewhere in detail (Mathieu-Costello 1987). Briefly, the entire vasculature was perfused with saline (11.06 g NaCl/L; 350 mosM; 20 000 USP units heparin/L). Perfusion fixation followed with a 6.25% solution of glutaraldehyde in 0.1 M sodium cacodylate buffer (total osmolality of the fixative, 1100 mosM; pH 7.4). All perfusions were performed at a nonpulsatile pressure of 80–90 mmHg (1 mmHg = 133 Pa). Two muscle samples (approximately 1 cm $\times$ 4 mm $\times$ 1 mm) of the red muscle were analyzed in each fish, as well as one white muscle sample (Table 1). All samples were taken from transverse sections of the fish at the level of the 8–10th spine of the first dorsal fin (Fig. 1). They were cut into thin longitudinal strips, stored in glutaraldehyde fixative (total osmolality, 1100 mosmol; pH 7.4), and processed for electron microscopy as previously described (Mathieu-Costello 1987).

Tissue sectioning

One-micrometre sections were cut on an LKB Ultratome III and stained with 0.1% aqueous toluidine blue solution. From each muscle sample, 4–8 blocks were cut into four transverse sections (angle between normal to section and fiber axis, $\alpha = 0^\circ$) and four longitudinal sections ($\alpha = \pi/2$), following procedures described elsewhere (Mathieu-Costello 1987). Sarcomere length, l_0 , was measured in each longitudinal section with a magnification of $\times 630$; 10 measurements of groups of consecutive sarcomeres were systematically sampled over the entire area of each section, then averaged.

Ultrathin sections (50–70 nm) were cut transversely to the muscle fiber axis in each sample. They were contrasted with uranyl acetate and bismuth subnitrate (Riva 1974). Electron micrographs for morphometry were taken on 70-mm films with a Zeiss 10 transmission electron microscope. Micrographs of a carbon grating replica (E. F. Fullam Inc., Schenectady, N.Y.) were recorded for calibration on each film.

Microcorrosion casts

We used the same procedures as in the previous study of pigeon flight muscle (Potter *et al.* 1991). Briefly, a modified Batson's No. 17 casting compound (Nopanitaya *et al.* 1979) was infused into the ventral aorta at a constant flow rate of 9 mL/min using a Harvard



FIG. 1. Example of a macroscopic view of a transverse section of skipjack tuna (animal 2, Tables 1–4) examined at the level of the 10th spine of the first dorsal fin. The specific sites (1, 3, 6) where samples were taken from this fish, as well as those examined in other animals (Table 1), are indicated. Note that even after the blood was washed out of capillaries during the fixation by perfusion, the red muscle is still very dark because of its high myoglobin content. See text for details on the relative area of red and white muscle in this section.

infusion pump. Following infusion of approximately 80 mL of casting material, the fish was left undisturbed for 30 min to allow polymerization to occur. Samples (approximately 1–3 cm) of the red muscle were taken in a transverse section of the fish at the level of the 7th spine of the first dorsal fin. They were digested away by 40% potassium hydroxide at 60°C for a few days, washed in distilled water, and air dried. Then they were mounted on stubs with conductive carbon cement, sputter coated with gold in a Technics Hummer II apparatus, and examined with a Cambridge Instrument Stereoscan 360 electron microscope.

Morphometry

Capillary counts per fiber sectional area in transverse and longitudinal sections, $Q_A(0)$ and $Q_A(\pi/2)$, respectively, were collected by point counting, using an eyepiece square grid test A 100 (see Weibel 1979 Appendix 3) on 1- μ m sections of plastic-embedded perfusion-fixed tissue examined at a magnification of $\times 400$ with a Leitz Ortholux microscope. On average, 17 ± 1 (transverse sections) and 24 ± 2 fields (longitudinal sections) were examined per sample, yielding totals of 1832 ± 119 and 293 ± 26 fiber profiles in transverse and longitudinal sections, respectively, per red muscle sample. In the white muscle, we examined a total of 15 and 18 fields in transverse and longitudinal sections, respectively. This yielded a total of about

200 (transverse) and 110 fiber profiles (longitudinal) in the sample. The point counts of capillary profile numerical density were collected, stored, and processed using an Apple computer. As in previous studies (Mathieu-Costello 1987), capillary density estimates were related to the muscle fibers as a reference space in all samples to avoid variation due to the unreliable preservation of the intercellular spaces by the preparation procedures.

The method used to estimate the degree of orientation, i.e., anisotropy of capillaries in each sample has been described elsewhere in detail (Mathieu *et al.* 1983). We first estimated the ratio between capillary counts per sectional area of transverse and longitudinal sections of muscle fibers, $Q_A(0)$ and $Q_A(\pi/2)$, respectively. This ratio was then used to calculate, via a table or graph of known coefficients, (i) the capillary orientation concentration parameter, K , and (ii) the coefficient $c(K,0)$ relating capillary counts per unit area of fiber in transverse sections, $Q_A(0)$, and capillary length per volume of muscle fiber, $J_V(c,f)$. Knowing $c(K,0)$, an estimate of $J_V(c,f)$ can be obtained by using the following equation:

$$[1] J_V(c,f) = c(K,0) \cdot Q_A(0)$$

which is based on the Fisher axial distribution of capillary segment orientation, relative to the axis of anisotropy (Mathieu *et al.* 1983). As described elsewhere (Mathieu *et al.* 1983; Mathieu-Costello 1987), the coefficient $c(K,0)$ is a direct indication of the amount of capillary length added by tortuosity and branching. For straight and unbranched capillaries, all parallel to the muscle fiber axis (perfect anisotropy), $K = \infty$ and $c(K,0) = 1$. For capillaries with no preferred orientation (isotropy), $K = 0$ and $c(K,0) = 2$, indicating that capillary length density is actually twice that given by a simple estimate of 'capillary density' in transverse sections, $Q_A(0)$.

Capillary diameter, $\bar{d}(c)$, fiber cross-sectional area, $\bar{a}(f)$, fiber cross-sectional perimeter, $\bar{b}(f)$, and capillary number around a fiber, N_{CAF} , were measured with an image analyzer (Videometric 150, American Innovision Inc.). On average, 154 ± 17 (SE) fibers were measured per sample. They were randomly selected on the same transverse sections used to estimate $Q_A(0)$. Capillary diameter, $\bar{d}(c)$, was obtained from circular profiles only (difference between smaller and longer diameters less than 15%). On average, 147 ± 5 (SE) capillary profiles were measured per sample. The selection of circular profiles to estimate $\bar{d}(c)$ assumed capillary cross-sectional circularity, based on our previous findings in rat muscles (Mathieu-Costello 1987).

Capillary–fiber ratio, $N_V(c,f)$ was computed as the product of capillary counts per fiber cross-sectional area, $Q_A(0)$, and fiber cross-sectional area, $\bar{a}(f)$.

Capillary–fiber perimeter ratio, in transverse section, $B_B(0)$ was estimated by intersection counting using the equation

$$[2] B_B(0) = l_c/l_f$$

where l_c and l_f are the intersections of test lines of a test grid with the boundaries of capillaries and fibers, respectively, in transverse sections. We used a 100-point square grid eyepiece system on the same sections used to estimate capillary number per fiber cross-sectional area, $Q_A(0)$. On average, 63 ± 4 (SE) fields were measured per sample examined at a magnification of $\times 1000$. Intersections were counted with both the horizontal and the vertical lines of the grid.

Capillary surface per fiber volume, $S_V(c,f)$, and capillary surface per fiber surface, $S_S(c,f)$, were estimated as (Mathieu-Costello *et al.* 1991)

$$[3] S_V(c,f) = J_V(c,f) \cdot \pi \cdot \bar{d}(c)$$

and

$$[4] S_S(c,f) = B_B(0) \cdot c'(K',0)$$

where $c'(K',0)$ is an anisotropy coefficient relating capillary perimeter per fiber cross-sectional area and capillary surface per volume of fiber. Except for muscles with a large degree of tortuosity of capil-

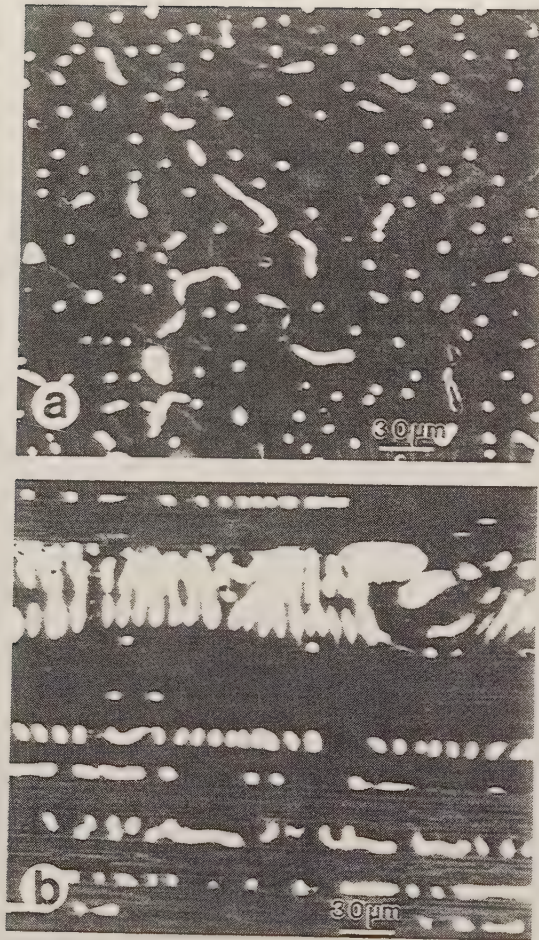


Fig. 2. Light micrographs of portions of muscle bundles in transverse (a) and longitudinal sections (b) of tuna red muscle. Capillaries are empty after the fixation by vascular perfusion. Note the large number of capillary branches running perpendicularly to the muscle fiber axis (b).

laries (coefficient $c(K,0) > 1.53$) the value of $c'(K',0)$ is 1. The maximal value of $c'(K',0)$ is 1.27 (for $c(K,0) = 2$; see Mathieu-Costello *et al.* 1991).

The volume density of mitochondria, myofibrils, and lipid droplets per volume of muscle fiber was estimated by standard point-counting procedure at a final magnification of $\times 22\,500$. Fourteen to sixteen micrographs were obtained by systematic sampling in one ultrathin transverse section from two randomly chosen blocks per sample in red muscle (total, 28–32 micrographs/sample) and four in the white muscle (total, 80 micrographs). Contact prints of the electron micrographic (EM) films were projected on a square grid test A 144 (see Weibel 1979 Appendix 3), using a microfilm reader (Documator DL 2, Jenoptic, Jena).

Mitochondrial volume per micrometre fiber length, $V_N(mt,f)$, was calculated as

$$[5] \quad V_N(mt,f) = V_v(mt,f) \cdot \bar{a}(f)$$

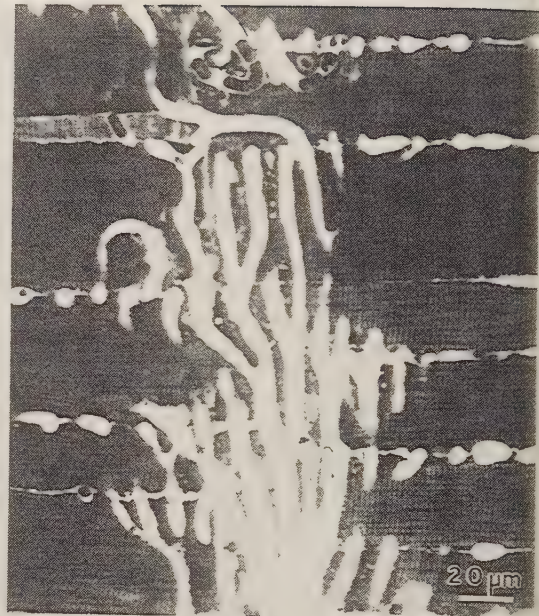


Fig. 3. Light micrograph of a section of a capillary manifold in tuna red muscle (compare with Fig. 4 in Potter *et al.* 1991).

Statistical analysis

Data are expressed as means $\pm$ SE. The standard errors of the estimates of capillary and mitochondrial density, as well as fiber cross-sectional area and perimeter, were calculated by pooling the data of the pictures from one sample (2–4 randomly chosen blocks cut transversely and (or) longitudinally) and applying formulas for the standard error of ratios. Therefore, the standard error indicates the variability between pictures at the sampling location analyzed in each sample. The standard error of the estimates of capillary diameter, $\bar{d}(c)$, and number around a fiber, N_{CAF} , indicates the variability between capillaries and fibers, respectively. Sample and group means were compared using the Student's *t*-test. Differences were taken as significant for $p < 0.05$.

Results

Figure 1 shows the macroscopic appearance of a transverse section of skipjack tuna after vascular perfusion fixation. The red muscle appeared very dark in spite of the washout of the red blood cells during the perfusion procedure (see Materials and methods and Fig. 2). This was due to the large myoglobin content of the muscle fibers. The cross-sectional areas of the red and white muscle (Fig. 1) were about 8 and 55 cm², respectively. The red muscle represented about 10% of the fish total cross-sectional area. Low-power light micrographs of transverse and longitudinal sections of perfused red muscle are shown in Figs. 2a and 2b. Transverse sections revealed a small fiber size and large capillary density (Fig. 2a) in all samples. As in pigeon flight muscle (Mathieu-Costello 1988 and 1991b), longitudinal sections of tuna red muscle showed straight capillaries running parallel to the muscle fibers, as well as capillaries oriented perpendicularly to the muscle fiber axis (Figs. 2b and 3). This suggested the presence of capillary manifolds in the muscles (compare Fig. 3 in this study with

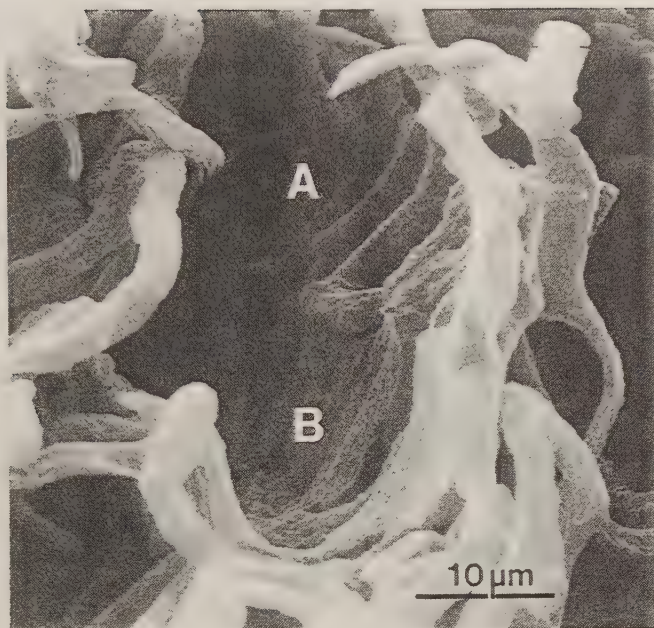


FIG. 4. Scanning electron micrograph of a cross-sectional view of a corrosion cast from tuna red muscle. Note the dense envelope formed by capillaries. Based on fiber dimensions (see Results), two muscle fibers (A and B) could be contained in the empty space. Micrograph taken by M. L. Costello.

TABLE 2. Morphometric estimates of degree of capillary geometry: counts in transverse ($Q_A(0)$) and longitudinal sections ($Q_A(\pi/2)$), orientation concentration parameter (K), anisotropy coefficient ($c(K,0)$), length density ($J_V(c,f)$), and surface per fiber volume ($S_V(c,f)$) in skipjack tuna muscle

Muscle No.	$Q_A(0)$ mm ⁻²	$Q_A(\pi/2)$ mm ⁻²	K	$c(K,0)$	$J_V(c,f)$ mm ⁻²	$S_V(c,f)$ mm ⁻¹
Red muscle						
1	3055±147	1791±76	1.03±0.13	1.47±0.05	4491±265	53.5±3.2
2	2686±161	1941±175	0.63±0.20	1.64±0.10	4405±377	49.3±4.3
3	2513±72	1495±85	1.00±0.13	1.48±0.05	3719±165	59.7±2.7
4	2421±79	1104±40	1.56±0.11	1.31±0.02	3172±114	53.7±2.0
5	3712±112	1669±112	1.59±0.17	1.31±0.04	4863±209	59.1±2.6
6	3476±176	2087±115	0.99±0.14	1.48±0.05	5144±313	57.5±3.6
7	2653±119	1454±67	1.17±0.13	1.42±0.04	3767±200	39.6±2.2
8	2524±94	1375±48	1.18±0.10	1.42±0.03	3584±153	39.1±1.7
$\bar{x}(n=8)$	2880±171	1615±114	1.14±0.11	1.44±0.04	4143±242	51.4±2.9
White muscle						
9	543±31	170±18	2.57±0.4	1.16±0.03	630±39	7.1±0.5

NOTE: Values are given as means ± SE. For muscle identification, see Table 1.

Fig. 4 in Potter *et al.* 1991). The examination of vascular casts by scanning electron microscopy showed capillaries forming a dense envelope of blood around portions of muscle fibers in tuna red muscle (Fig. 4).

Sarcomere length, fiber cross-sectional area, capillary number per fiber cross-sectional area, and capillary diameter are given in Table 1. Sarcomere length ranged from 1.72 to 1.87 μm in the samples. The average fiber cross-sectional area of $560 \pm 30 \mu\text{m}^2$ yielded an equivalent circular fiber diameter

of $27 \pm 1 \mu\text{m}$ in red muscle. Capillary number per fiber cross-sectional area was $2880 \pm 171 \text{ mm}^{-2}$. In white muscle, fiber size was about 8 times greater than, and capillary density was about 5 times lower than, that of red muscle (Table 1). Mean capillary diameter ranged from 3.35 to 5.39 μm (Table 1) in red muscle. It was 3.6 μm in the white muscle sample.

Morphometric estimates of capillary orientation coefficients, K and $c(K,0)$, and capillary length and surface per fiber volume, $J_V(c,f)$ and $S_V(c,f)$, respectively, are given in Table 2. The

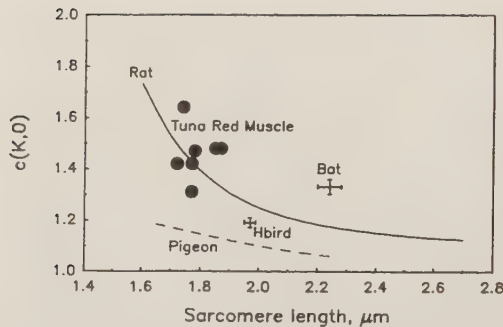


FIG. 5. Plot of anisotropy coefficient $c(K,0)$, relating $Q_A(0)$ to $J_V(c,f)$, against sarcomere length in tuna red muscle, and group mean values in bat (Mathieu-Costello *et al.* 1992b) and hummingbird (Hbird) flight muscles (Mathieu-Costello *et al.* 1992a). Relationships between $c(K,0)$ and sarcomere length in rat hindlimb ($n = 42$) (Mathieu-Costello *et al.* 1991) and pigeon pectoralis muscle (Mathieu-Costello 1991b) are shown by the solid and broken lines, respectively.

narrow range of sarcomere length, l_0 , in the samples did not allow us to examine the relationship(s) between the orientation coefficients and fiber shortening, i.e., reduction in sarcomere length. Comparison with data from previous studies showed that the values of $c(K,0)$ in tuna red muscle were similar to those previously found in rat hindlimb muscles examined at similar sarcomere length (Fig. 5, solid line). For comparison, the curvilinear relationship between $c(K,0)$ and l_0 in pigeon and mean group values in bat pectoralis and hummingbird pectoralis and supracoracoideus muscles are also shown in Fig. 5. As mentioned in the Materials and methods section, the coefficient $c(K,0)$ is an index of the amount of capillary length added by tortuosity and branching. In red muscle, capillary length per volume of muscle fiber ($\bar{x} = 4143 \pm 242 \text{ mm}^{-2}$) was 44% larger than a simple estimate of 'capillary density' in transverse sections, $Q_A(0)$, would indicate (the group mean value of the $c(K,0)$ was 1.44 ± 0.04 , Table 2; see eq. 1). In the white muscle sample, $c(K,0)$ was 1.16 ± 0.03 and $J_V(c,f)$ was 630 mm^{-2} . $S_V(c,f)$ ranged from 39.1 to 59.7 mm^{-1} in red muscle. It was 6–9 times smaller in white muscle (Table 2).

The low-power electron micrograph shown in Fig. 6 illustrates the abundance of mitochondria in the muscle fibers of tuna red muscle. Table 3 gives morphometric data on fiber ultrastructure. In red muscle, mitochondria occupied from 24 to 32% of the muscle fiber volume. About one-sixth (muscle 7) to more than one-third (muscles 1–3) of the total volume of mitochondria was subsarcolemmal. The fractional volume of subsarcolemmal mitochondria varied greatly among sampling sites in 2 out of 4 animals (Table 3; muscles 3–4 and 7–8). Mitochondrial volume density was about 10 times lower in the white muscle (Table 3). The volume of lipid droplets per volume of muscle fiber ranged from 0 to 2% and also varied greatly between samples in the same animal (Table 3; muscles 1–2, 3–4, and 5–6); in several red muscle samples (muscles 1, 6–8), it was as low as in the white muscle sample (Table 3). Figure 7 shows the plot of $J_V(c,f)$, against mitochondrial volume density, $V_V(mt,f)$, in the samples. For comparison, the linear regression between $J_V(c,f)$ and $V_V(mt,f)$ in bat and rat muscles, as well as mean group values in hummingbird, bat, and rat muscles are shown in Fig. 7.

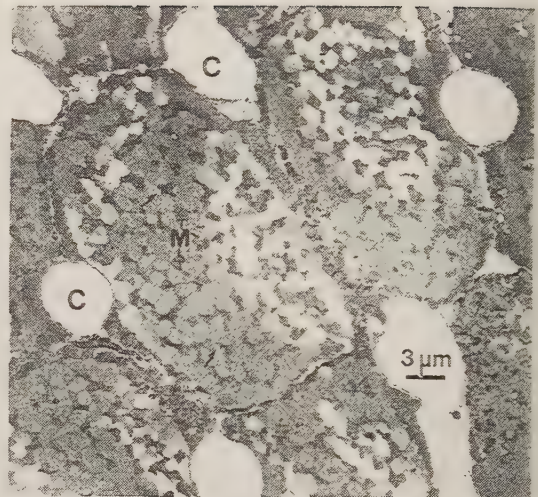


FIG. 6. Electron micrograph of transverse section of muscle fibers and adjacent capillaries (C) and skipjack tuna red muscle. Note the large density of mitochondria (M) and relatively few lipid droplets (arrows) in the muscle fibers.

Capillary surface per volume of mitochondria, i.e., the ratio between $S_V(c,f)$ (Table 2) and $V_V(mt,f)$ (Table 3) was $180 \pm 7 \text{ mm}^2/\text{mm}^3$ in red muscle, and $254 \pm 33 \text{ mm}^2/\text{mm}^3$ in white muscle. The surface of inner mitochondrial membrane per unit volume of mitochondria was $63\,000$ (subsarcolemmal) and $71\,000 \text{ mm}^2/\text{mm}^3$ (interfibrillar mitochondria) in red muscle and was $31\,000 \text{ mm}^2/\text{mm}^3$ in white muscle (Moyes *et al.* 1992). This yields a capillary surface per unit surface area of inner mitochondrial membrane of about 2.6×10^{-3} (red muscle) and 8.2×10^{-3} (white muscle). Thus, the aggregate surface of inner mitochondrial membrane was about 400 times (red muscle) and 125 times (white muscle) greater than capillary surface area. The surface areas of mitochondrial outer membrane were 7500 and $4700 \text{ mm}^2/\text{mm}^3$ in red and white muscle, respectively (O. Mathieu-Costello, unpublished data). Thus, capillary surface per unit surface area of outer mitochondrial membrane was 0.024 (red muscle) and 0.054 (white muscle). In red muscle the aggregate surface area of outer mitochondrial membrane was about 10 times smaller than inner mitochondrial membrane surface area, and about 40 times greater than capillary surface area. In white muscle the aggregate surface area of outer mitochondrial membrane was about 7 times smaller than inner mitochondrial membrane surface area and about 20 times greater than capillary surface area.

Estimates of capillary–fiber morphometrics and mitochondrial volume per fiber in each sample are given in Table 4. Capillary–fiber perimeter ratio ranged from 0.26 to 0.34 in red muscle. It was about one-fourth these values in white muscle. The number of capillaries around each fiber, N_{CAF} , was similar in red (range 4.43–5.36) and white muscle (4.77) in spite of the 8-fold difference in fiber size between the muscles (Table 1). The capillary surface anisotropy coefficient, $c'(K',0)$, had a value of 1 (i.e., capillary–fiber perimeter ratio, $B_B(0)$, was a direct estimate of capillary surface per fiber surface, $S_S(c,f)$) in all samples except one. In muscle 2,

TABLE 3. Morphometric estimates of fiber ultrastructure: volume density of total ($V_V(\text{mt},f)$), subsarcolemmal ($V_V(\text{ms},f)$), and interfibrillar ($V_V(\text{mi},f)$) mitochondria, and volume density of intracellular lipids ($V_V(\text{li},f)$) and myofibrils, ($V_V(\text{my},f)$)

Muscle No.	$V_V(\text{mt},f)$ (%)	$V_V(\text{ms},f)$ (%)	$V_V(\text{mi},f)$ (%)	$V_V(\text{li},f)$ (%)	$V_V(\text{my},f)$ (%)
Red muscle					
1	29.9±1.6	11.4±1.5	18.5±0.9	0.1±0.0	66.0±1.9
2	30.5±1.6	12.3±2.1	18.2±0.9	1.1±0.3	61.4±1.5
3	32.4±1.9	12.3±2.4	20.1±1.0	0.9±0.3	64.6±2.1
4	26.0±1.5	5.4±1.5	20.6±0.9	2.0±0.5	69.0±1.6
5	29.8±1.1	7.9±1.3	21.8±0.9	1.7±0.4	67.4±1.5
6	29.6±1.4	8.5±1.7	21.1±0.7	0.0±0.0	66.4±1.5
7	24.4±0.6	4.2±0.8	20.2±0.8	0.0±0.0	68.9±1.2
8	25.1±1.1	8.1±1.2	17.1±0.6	0.0±0.0	65.2±1.5
$\bar{x}(n = 8)$	28.5±1.0	8.8±1.1	19.7±0.6	0.7±0.3	66.1±0.9
White muscle					
9	2.8±0.3	0.7±0.2	2.1±0.2	0.1±0.0	69.3±1.0

NOTE: Values are given as means ± SE. For muscle identification, see Table 1.

TABLE 4. Data relating capillary-fiber morphometrics to mitochondrial amount per micrometre length of fiber ($V_N(\text{mt},f)$) in skipjack tuna muscle: fiber perimeter ($\bar{b}(f)$), capillary-fiber perimeter ratio in transverse sections ($B_B(0)$), capillary-fiber number ratio ($N_N(c,f)$), and capillary number around a fiber (N_{CAF})

Muscle No.	$\bar{b}(f)$ (μm)	$B_B(0)$	$V_N(\text{mt},f)$ (μm^3)	$N_N(c,f)$	N_{CAF}
Red muscle					
1	108±3	0.26±0.01	170±15	1.74±0.15	5.32±0.16
2	113±4	0.27±0.01	196±14	1.73±0.13	5.36±0.18
3	114±3	0.34±0.01	187±13	1.45±0.07	4.43±0.10
4	124±3	0.34±0.01	184±13	1.72±0.09	4.72±0.10
5	100±2	0.31±0.01	139±6	1.73±0.06	5.12±0.13
6	98±3	0.31±0.01	136±10	1.59±0.12	5.16±0.12
7	102±3	0.29±0.01	132±6	1.44±0.08	5.16±0.15
8	100±3	0.30±0.01	129±6	1.29±0.06	4.47±0.12
$\bar{x}(n = 8)$	107±3	0.30±0.01	159±10	1.59±0.06	4.97±0.13
White muscle					
9	253±1.0	0.07±0.01	117±13	2.28±0.16	4.77±0.21

NOTE: Values are given as means ± SE. For muscle identification, see Table 1.

the value of $c(K,0)$ was 1.64 (Table 2). This yielded a $c'(K',0)$ of 1.05 in that sample (see Mathieu-Costello *et al.* 1991 for the estimation of $c'(K',0)$). Thus, $S_S(c,f)$ was 5% larger than $B_B(0)$ in the sample (see eq. 4). The plot of $S_S(c,f)$ against mitochondrial volume per micrometre length of fiber, $V_N(\text{mt},f)$ is shown in Fig. 8. For comparison, the linear regression between $S_S(c,f)$ and $V_N(\text{mt},f)$ in rat soleus muscle is also shown (broken line), as well as group averages in bat muscles and hummingbird flight muscle.

Discussion

Small fiber size, high capillary numerical density, and high mitochondrial volume density are well established characteristics of tuna red muscle (Bone 1978; George and Stevens 1978; Hulbert *et al.* 1979; Dickson 1988). In this study, we used recently developed morphometric methods to quantify the geometry of blood-tissue exchange in tuna. We characterized the structural potential for O_2 delivery to the muscle fibers

(capillary length and surface area) and examined the relationship(s) between capillarity and fiber mitochondrial volume. Comparison with highly aerobic muscles of birds and mammals revealed both similarities and striking differences in capillary-fiber structural relationships in tuna red muscle.

Fiber size

The average fiber circular diameters of 27 ± 1 (SE) μm (red muscle), and about 73 μm (white muscle) are smaller than or similar to those previously reported in tuna muscle after fixation by immersion in glutaraldehyde solution and processing for electron microscopy. Bone (1978) measured mean fiber diameters of 31 and 100 μm in skipjack red and white muscle, respectively. George and Stevens (1978) reported values of 34.58 ± 6.16 (SD) (red muscle) and 66.03 ± 11.59 (SD) μm (white muscle) in kawakawa, *Euthynnus affinis*. Looking at individual fiber dimensions, Hulbert *et al.* (1979) found a vast range of fiber diameters both in red (12–52) and white (20–110 μm) tuna muscle. Based on our previous comparisons with

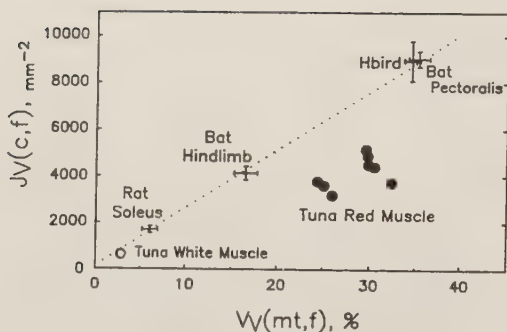


FIG. 7. Plot of capillary length per fiber volume, $J_V(c,f)$, against mitochondrial volume per volume of muscle fiber, $V_V(mt,f)$, in tuna red muscle (●) and white muscle (○). Linear regression in bat and rat muscles (broken line, $J_V(c,f) = 249 \cdot V_V(mt,f) + 142$; $r = 0.993$) and group mean values in bat hindlimb and pectoralis muscle and in rat soleus muscle are from Mathieu-Costello *et al.* (1992b); group mean value in hummingbird (Hbird) pectoralis and supracoracoideus muscles is from Mathieu-Costello *et al.* (1992a).

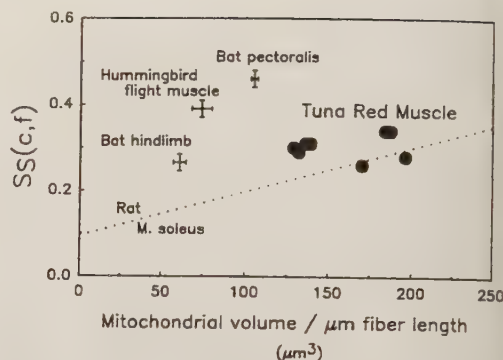


FIG. 8. Correlation between capillary surface per fiber surface, $S_S(c,f)$, and mitochondrial volume per micrometre fiber length, $V_N(mt,f)$, in tuna red muscle (●). Linear regression in bat and rat muscles (broken line, $S_S(c,f) = 0.0010 \cdot V_N(mt,f) + 0.1$; $r = 0.67$) and group mean values in bat hindlimb and pectoralis muscle are from Mathieu-Costello *et al.* (1992b); group mean value in hummingbird flight muscles (pectoralis and supracoracoideus) is from Mathieu-Costello *et al.* (1992a).

material prepared for histochemistry (see Mathieu-Costello *et al.* 1992b), we expect a minimal amount of tissue shrinkage during the fixation and preparation procedure used in this study compared with muscle *in situ*. The amount of tissue shrinkage in freshly frozen tissue processed for histochemistry is known to be minimal (Brodal *et al.* 1977). In various fish specimens, including *Katsuwonus* and *Euthynnus*, Dickson (1988) reported average fiber diameters of 30–35 and 65–70 μm in red and white muscle processed for histochemistry. This suggests that the above differences between studies are not likely to be related to tissue shrinkage during preparation. Besides interanimal and (or) interspecies variability, a source of variation in fiber cross-sectional area is the variable amount of fiber shortening during sample removal from intact muscles (see Mathieu-Costello *et al.* 1989). To our knowledge, this is the first study in which tuna muscles were fixed by vascular perfusion-fixation, i.e., *in situ* fiber length was preserved. The average sarcomere length values in the samples (Table 1) are within the range of *in situ* sarcomere lengths measured in red and white muscle of coalfish (Patterson and Goldspink 1972). We are not aware of any report of sarcomere length in excised muscles of tuna.

In axial musculature of African lungfish, Dunn *et al.* (1981) measured sarcomere lengths of 1.5 and 2.0 μm for red and white muscle, respectively. Average fiber diameter at 2.1 μm sarcomere length was 20 in red and 66 μm in white muscle (calculated from Dunn *et al.* 1981) compared with 25 (red muscle) and 68 μm (white muscle) in tuna (calculated from data in Table 1), suggesting that fiber size in tuna muscle is not the lowest among fish. Other reported values for fiber cross-sectional area in fish red muscle (no sarcomere length indicated) ranged from 471 μm^2 in trout (Johnston and Moon 1980) to 1115 μm^2 in highly aerobic fibers of anchovy (Johnston 1982b). Thus, fiber size in tuna red muscle was not particularly small compared with other fish, and a small fiber size is not necessarily a characteristic of highly aerobic fibers in fish (mitochondrial volume density in anchovy red muscle was very high; see below). In tuna red muscle, fiber cross-sectional area was similar to that of aerobic fibers in pigeon

flight muscle (Mathieu-Costello 1991b), bat flight muscle, and bat hindlimb (Mathieu-Costello *et al.* 1992b) at a similar sarcomere length. The cross-sectional area of tuna red muscle fibers was about 4 times smaller than in rat soleus muscle (Mathieu-Costello 1987), 3–4 times smaller than in dog gastrocnemius muscle (Mathieu-Costello 1991a), and 2–4 times greater than in hummingbird pectoralis and supracoracoideus muscle (Mathieu-Costello *et al.* 1992a).

The length of thick and thin filaments muscle was 1.45 ± 0.02 and 1.75 ± 0.03 μm (red muscle) and 1.43 ± 0.03 and 1.67 ± 0.03 μm (white muscle), respectively. The values in red muscle are very close to those in hummingbird flight muscle similarly prepared (Mathieu-Costello *et al.* 1992a). The values for thick filament are consistent with those reported in fish (Akster 1981; Sosnicki *et al.* 1991), rat (Walker and Schrodt 1969; Mathieu-Costello 1987), and bat muscles (Mathieu-Costello *et al.* 1992b) after glutaraldehyde fixation. These data support the idea of a constant myosin filament length in muscles of vertebrates. The values for thin filaments are similar to that reported in white and pink fibers of perch (Akster 1981). They are smaller than in fixed red and white muscle of carp (Sosnicki *et al.* 1991), rat (Walker and Schrodt 1969), or bat (Mathieu-Costello *et al.* 1992b), and living rat muscles (Close 1972). Variations in the length of thin filaments have been reported in crustacean (Franzini-Armstrong 1970) and fish muscles (Akster 1981). To our knowledge, filament length in tuna has never been reported. Shorter filament lengths allow faster rates of contraction (Franzini-Armstrong 1970; Akster 1981; Otten 1987) and may have implications in contraction velocity rates in tuna. The relationship(s) between filament length, functional sarcomere length range, and contraction velocity in red and white muscle of tuna at different swimming speeds is (are) not known.

Capillarity

The average number of capillaries around a fiber, N_{CAF} , in red and white muscle (Table 4) was very close to that previously reported in skipjack tuna red muscle (4.75; Bone 1978). Notice that there are approximately the same number of capil-

larities around each fiber in red and white muscle (Table 4) in spite of the large difference in fiber size (Table 1). Larger values for N_{CAF} have been reported in other fish (e.g., 5.3–6.6 in red muscle of flathead, *Platycephalus bassensis*, Mosse 1978). Compared with highly aerobic muscle of birds and mammals, the number of capillaries around a fiber was the same in tuna red muscle as in hummingbird flight muscle, in which fiber size was substantially smaller (Mathieu-Costello *et al.* 1992a). It was significantly smaller than in bat pectoralis muscle (5.63 ± 0.23) and rat soleus muscle (5.96 ± 0.35), i.e., in muscles with smaller (bat pectoralis muscle) or substantially larger fiber size (rat soleus muscle; Mathieu-Costello *et al.* 1992b).

We are not aware of any report of capillary density (e.g., capillary–fiber ratio or capillary number per fiber cross-sectional area) or geometry in tuna muscle. When compared with red muscle of various species of fish with similar fiber size (e.g., Mosse 1979), tuna capillary–fiber ratio was high (1.29–2.28; Table 4) but not the highest for fish. Similar or greater values have been found in fish red muscle with larger fiber size. For example, capillary–fiber ratios of 1.87–2.45 were reported in flathead red muscle (Moose 1978). In 28°C-acclimated carp it was 2.2 ± 0.1 and increased to 4.8 ± 0.2 with acclimation to 2°C (Johnston 1982a). For comparison, capillary–fiber ratio in hummingbird flight muscle was 1.55 ± 0.06 . It was 2.02 ± 0.10 and 1.24 ± 0.06 in bat pectoralis muscle and hindlimb, respectively, and 2.59 ± 0.24 in rat soleus muscle.

Except for slow muscle of anchovy, in which substantially higher capillary density has been reported (Johnston 1982b), capillary number per fiber cross-sectional area in tuna red muscle (Table 1) was among the highest in fish muscles (for review see Egginton and Johnston 1983). In slow muscle of Conger eel fixed at an average sarcomere length of 2.3 μm , Egginton and Johnston (1983) measured an anisotropy coefficient, $c(K,0)$, of 1.016. Such a high degree of capillary orientation was possibly related to the large number of anastomoses in the muscle (Egginton and Johnston 1983). Tuna red muscle also showed a high number of capillary branches running perpendicularly to the muscle fiber axis (Figs. 2b, 3, and 4). However, the capillary orientation coefficient ($c(K,0)$; Fig. 5 and Table 2) was substantially higher than previously reported in fish muscle. Besides a direct effect of sarcomere length on capillary anisotropy (Fig. 5), it is possible that differences in capillary branching between Conger eel and tuna muscles account for the difference in $c(K,0)$ values. In pigeon pectoralis muscle, the degree of anisotropy of capillaries was much lower than in tuna or rat muscle fixed at similar sarcomere length (Fig. 5). The large difference in $c(K,0)$ values between muscles shows the importance of considering capillary geometry when comparing the size of the capillary network in muscles. Londraville and Sidell (1990) also measured high $c(K,0)$ values (1.73 and 1.45) in red muscle samples of two antarctic fish, *Trematomus newnesi* and *Notothenia gibberifrons*, respectively. In tuna red muscle (this study), capillary tortuosity and branching added an average of 1267 mm^{-2} to capillary length per fiber volume compared with straight capillaries oriented strictly parallel to the muscle fibers. In pigeon pectoralis muscle fixed at approximately the same sarcomere length (muscle 1 in Mathieu-Costello 1991b), the product of $Q_A(0)$ and $(c(K,0) - 1)$ was 520 mm^{-2} .

Mitochondrial density

There are numerous reports of mitochondrial volume density in fish muscle (for review see Dunn *et al.* 1981). The

value of 35% reported by Hulbert *et al.* (1979) for tuna red muscle is greater than the range of mitochondrial volume densities we found in this study. In white muscle, mitochondrial volume density was 2.8% (this study) compared with 2% reported by Hulbert *et al.* 1979. High mitochondrial densities (20–30%) have been reported in red muscle of a number of fish species, including shark (Kryvi 1977), eel (Hulbert and Moon 1978), trout, and carp (Johnston and Moon 1981). The highest mitochondrial volume density for fish (45.5%) was found in anchovy red muscle (Johnston 1982b).

Capillarity and O_2 demand

It is interesting that in tuna red muscle, the linear regression of $J_V(c,f)$ and $V_V(mt,f)$, $r = 0.52$ ($J_V(c,f) = 123 \cdot V_V(mt,f) + 619$), yielded a capillary length per fiber volume of 4309 mm^{-2} at 30% mitochondrial density. This value of $J_V(c,f)$ is about one-half that in bat muscles at the same mitochondrial volume density (Fig. 7). Comparison with data obtained for capillary and mitochondrial density in a number of species of fish (for review see Egginton and Johnston 1983) is not possible because sarcomere length and capillary orientation were not reported. Both capillary number per fiber cross-sectional area, $Q_A(0)$, and $c(K,0)$ depend on sarcomere length, and the estimation of $J_V(c,f)$ requires knowledge of capillary orientation (see eq. 1). In two studies in which the degree of orientation of capillaries was estimated, capillary length per fiber volume at a given mitochondrial volume density in the muscle fibers was substantially smaller than in tuna red muscle. In red muscle of Conger eel, $J_V(c,f)$ was 625 mm^{-2} for a fiber mitochondrial volume density of 22.7% (Egginton and Johnston 1983). In antarctic fish in which mitochondrial volume density distributions in the muscle fibers ranged from 20 to 40%, $J_V(c,f)$ averaged 505–639 mm^{-2} (Londraville and Sidell 1990).

At a given mitochondrial volume per fiber, the average number of capillaries around a fiber, (N_{CAF}), was also smaller in tuna red muscle than in highly aerobic muscles of birds and mammals. The linear regression between N_{CAF} and mitochondrial volume per micrometre length of fiber, $V_V(mt,f)$, in bat pectoralis muscle, bat hindlimb, and rat soleus muscle yields mean group values for N_{CAF} of 6.58 ± 0.20 (bat pectoralis muscle), 5.64 ± 0.15 (bat hindlimb) and 6.45 ± 0.28 (rat soleus muscle) at 159 μm^3 mitochondrial volume per fiber (calculated from Mathieu-Costello *et al.* 1992b). The mean group value for tuna red muscle at a similar mitochondrial volume per fiber (Table 4) was significantly smaller. As for bat and rat muscles, the average number of capillaries around a fiber in hummingbird pectoralis and supracoracoideus muscles at a given mitochondrial volume per fiber was also significantly higher than in tuna.

In tuna red muscle, capillary surface per fiber surface (0.30 ± 0.01 at 159 μm^3 mitochondrial volume per fiber, Table 4) was not significantly different from that in rat soleus (0.32 ± 0.02) at the same mitochondrial volume per fiber of 159 μm^3 (calculated from Mathieu-Costello *et al.* 1992b). In bat pectoralis muscle, capillary surface per fiber surface was about twice that found in tuna red muscle at a similar mitochondrial volume per fiber (Fig. 8). There have been several reports of capillary contact length, fiber perimeter, fiber cross-sectional area, and mitochondrial volume density in fish muscles, including anchovy red muscle, which has the highest reported mitochondrial volume density for fish (Johnston 1982b). Percent capillary–fiber contact, i.e., the ratio between capillary contact length and fiber perimeter is an equivalent measurement to the stereological estimate of capillary–fiber perimeter

ratio, $B_B(0)$; see Mathieu-Costello *et al.* 1991. Capillary-fiber percent contact length was 31% in hagfish (Flood 1979), 23% in shark (Totland *et al.* 1981), and 51% in anchovy (Johnston 1982b). Thus, the 30% value in tuna red muscle (Table 4) was not the highest for fish muscle. Capillary surface (μm^2) supplying $1 \mu\text{m}^3$ of mitochondria was 0.06 in shark (Totland *et al.* 1981) and 0.18 in anchovy (Johnston 1982b). In tuna red muscle, the value of this variable (i.e., $B_B(0) \cdot \bar{b}(f)/V_N(\text{mt}, f)$) was 0.20 ± 0.02 . This underscores the importance of considering fiber size when comparing the relationship(s) between capillarity and mitochondrial volume in muscles. In anchovy, mitochondrial volume density (45%) and capillary-fiber surface ratio (51%; Johnston 1982b) were almost 2 times higher than in tuna red muscles. Capillary contact length per fiber in anchovy ($91.6 \pm 5.1 \mu\text{m}$) was 3 times greater than in tuna ($B_B(0) \cdot \bar{b}(f) = 32.1 \pm 1.4 \mu\text{m}$). Besides differences in capillary-fiber surface ratio, the difference in capillary contact length was due to the different fiber size in the muscle. Fiber cross-sectional area was about 2 times greater in anchovy (Johnston 1982b) than in tuna red muscle. As a result, mitochondrial volume per micrometre length of fiber, $V_N(\text{mt}, f)$, was substantially greater in anchovy ($507 \mu\text{m}^3$; calculated from Johnston 1982b) than in tuna ($159 \mu\text{m}^3$). However, capillary surface per unit volume of mitochondria in the muscle fibers was very close in the two muscles.

Functional implications

Obviously, a number of functional variables including operating temperature, blood flow, functional hematocrit, and blood O_2 -carrying capacity affect O_2 delivery to the muscle fibers. From a structural point of view, the arrangement of the capillary network in tuna red muscle resemble that of highly aerobic muscles of bird (pigeon pectoralis, and hummingbird pectoralis and supracoracoideus muscles) in that evidence of capillary manifolds was found. Such an arrangement that increases capillary surface at the venular end of the network where O_2 tension is lower will enhance O_2 delivery to the muscle fibers (Potter *et al.* 1991). Gaetgens *et al.* (1981a, 1981b) suggested that a different capillary architecture in bird muscles may compensate for the less favorable rheological properties of nucleated red cells. Hughes *et al.* (1982) found red blood cells of a teleost fish, the yellowtail *Seriola quinqueradiata*, less deformable than human red cells when compared at their normal environmental temperature. To our knowledge there are no available data on tuna red cell deformability. In skipjack tuna, red cells are nucleated as in other fish and they are rather large (short axis: $7.40 \pm 0.07 \mu\text{m}$; long axis, $9.61 \pm 0.05 \mu\text{m}$). Thus, the presence of capillary manifolds in bird and tuna muscles could be related to the larger size and lesser deformability of their red blood cells compared with those of mammals. It could also be implicated in the transfer of heat. It is well known that tuna red muscle operates at higher than ambient water temperature by conserving heat in the counter-current system of the central rete (Stevens and Neill 1978). Cold arterial blood coming from the gills is warmed up by venous blood returning from the muscle. It is possible that the particular arrangement of capillaries in tuna red muscle favours heat recovery from the muscle at the venular end of the network, as it possibly favors heat removal in bird flight muscle.

Capillary surface per fiber surface at given mitochondrial volume per muscle fiber was approximately 50% lower than that of bat and hummingbird flight muscle, and it was not significantly different from that of rat soleus muscle. Moyes *et al.* (1992) measured maximal respiratory rates of $2.6 \mu\text{mol}$

$\text{O}_2/(\text{min} \cdot \text{g}$ of muscle) in tuna red muscle mitochondria at 25°C *in vitro*. If we consider that 1 g of tuna red muscle consists of about 0.80 cm^3 of fibers (see Suarez *et al.* 1991), we find that it contains $0.80 \cdot 0.285 = 0.23 \text{ cm}^3$ of mitochondria. These values and the above mitochondrial respiratory rate per gram of tissue yield a maximal mitochondrial respiratory rate in tuna muscle *in situ* of $0.22 \text{ mL O}_2/(\text{min} \cdot \text{mL mitochondria})$. This value is considerably smaller than that estimated in locomotory muscles of mammals running at $\dot{V}\text{O}_{2\text{MAX}}$ ($3-5 \text{ mL O}_2/(\text{min} \cdot \text{mL mitochondria})$; Schwerzmann *et al.* 1989) and in flying hummingbird ($7-10 \text{ mL O}_2/(\text{min} \cdot \text{mL mitochondria})$; Suarez *et al.* 1991). Mitochondrial maximal respiratory rates *in vitro* are known to be lower than those estimated *in vivo* (see Suarez *et al.* 1991). However, we do not expect the above differences in maximal respiratory rates between tuna, mammals, and birds to be solely due to differences between *in vitro* and *in vivo* measurements. Maximal *in vitro* rates for hummingbird flight muscle mitochondria were 39% of those estimated *in vivo* during hovering flight (Suarez *et al.* 1991). *In vitro* maximal rates of cat muscle mitochondria were 62% of the highest rates estimated *in vivo* (Schwerzmann *et al.* 1989). A number of unknowns, including tuna maximal O_2 consumption and red muscle contribution to O_2 uptake at $\dot{V}\text{O}_{2\text{MAX}}$ preclude the estimation of red muscle mitochondria maximal respiratory rates *in vivo*. If we assume *in vitro* measurements to be as low as 25% of those achievable *in vivo*, maximal respiratory rate of red muscle mitochondria in tuna ($0.9 \text{ mL O}_2/(\text{min} \cdot \text{mL of mitochondria})$) is about 3-5 times lower than in mammals and 7-10 times lower than in hummingbird. Why the maximum (state 3) respiratory capacities of tuna mitochondria are lower than those found with mammalian or avian muscle preparations is not clear. One possible explanation is that the muscles operate at a different temperature. While it is believed that wild skipjack tuna have excess core temperatures of $1-2^\circ\text{C}/\text{kg}^{0.6}$ during normal swimming, the amount by which core temperature increases during burst activity is not clear (Stevens and Neill 1978). Assuming Q_{10} values are about 2.5-3 for mitochondrial respiratory rates (Hochachka and Somero 1984), a 10°C increase in operating temperature would yield values for maximal mitochondrial respiratory rates in tuna close to those found in mammals. Interestingly, excess core temperatures of 8.6°C (white muscle) and 9.1°C (red muscle) have been observed in one group of skipjack tuna (Stevens and Neill 1978). Another implication is that fish muscle mitochondria may be designed for functions other than simply oxidative phosphorylation. For example, protein and amino acid metabolism is up-regulated in fish muscle compared with other vertebrates (Hochachka and Somero 1984). Possibly, the high mitochondrial volume densities observed may be required for the enzymes of amino acid and protein turnover. The great size of the capillary-fiber interface in tuna may also be related to functions other than O_2 per se, for example, substrate and (or) heat transfer between capillaries and muscle fibers.

Acknowledgments

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Abstract. – Five submersible dives were conducted to evaluate the behavior of deepwater shrimp and the relationship of their density to bottom type and trap yield. Differences in behavior of two species of *Heterocarpus* were observed: *H. ensifer* tended to group around large anemones and other benthic relief over otherwise flat, sandy bottom and were very active in the presence of a baited container; whereas *H. laevigatus* were solitary and showed little activity around a baited container. Greater densities of *H. laevigatus* were observed on volcanic than on coralline substrate, indicating a possible association with this bottom type. Trap catches were regressed against observed *H. laevigatus* densities yielding an estimate of the catchability coefficient. This coefficient differed from that obtained from a previously conducted Leslie model depletion study. Factors contributing to this difference may include comparing estimates of catchability based on data from different areas, bias in the estimate of catchability based on observed density, and bias in the estimate of catchability from the depletion study. A combined fishing and visual census study is suggested as the best assessment technique.

An assessment of the exploitable biomass of *Heterocarpus laevigatus* in the main Hawaiian Islands. Part 2: Observations from a submersible

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Tropical deepwater pandalid shrimp have potential for commercial harvesting in many areas of the Pacific (Struhsaker and Aasted 1974, Wilder 1977, Moffitt 1983, King 1984, Tagami and Barrows 1988). These shrimp are readily trapped but not easily trawled (Struhsaker and Aasted 1974). The largest and most commercially desirable species in Hawaii is *Heterocarpus laevigatus* (Tagami and Barrows 1988); the smaller *H. ensifer* has less commercial appeal but is also abundant (Struhsaker and Aasted 1974). In the early 1980s, several boats initiated a trap fishery targeting *H. laevigatus*, and landings rose to a high of 159 metric tons (t) in 1984 (HDLNR 1986). By 1985, most vessels left the fishery, and the annual landings dropped to <6 t/yr (West. Pac. Fish. Inf. Network, NMFS Honolulu Lab., unpubl. data).

Early predictions of maximum sustainable yield for Hawaiian shrimp, based on little or no direct data, were as much as 1000–2000 t/yr (Struhsaker and Aasted 1974, HDLNR 1979). Recent research on population dynamics combined with systematic trapping surveys has resulted in more refined estimates of exploitable biomass and maximum sustainable yield for *H. laevigatus* in various island locations (Dailey and Ralston 1986, Ralston 1986, Moffitt and Polo-

vina 1987, Ralston and Tagami 1992). The most recent estimate of exploitable biomass for the main Hawaiian Islands, 271–1050 t, is based on an estimate of the catchability coefficient (q) obtained through a Leslie model depletion study, coupled with catch-per-unit-effort (CPUE) values and habitat area estimates obtained through systematic trapping (Ralston and Tagami 1992).

The relationship of observed target-species density to fishing-gear CPUE has been used to estimate stock biomass and catchability (Ralston et al. 1986, Kulbicki 1988). Estimates of abundance obtained through visual census techniques are generally higher than those based on catches of fishing gear, and the relative reliability of the various assessment methods must be analyzed on a case-by-case basis (Uzmann et al. 1977, Powles and Barans 1980, Kulbicki and Wantiez 1990, Matlock et al. 1991).

In the present study, we conducted submersible dives at several sites in the Hawaiian Islands to observe shrimp behavior both away from and in the vicinity of a baited container and to record density and substrate associations of *H. laevigatus*. Observations of shrimp behavior and substrate associations have applications to commercial fishermen in terms of

trapping technique and site selection. The mean of observed densities recorded during submersible dives is regressed against yields of a trap set at the dive sites to obtain an estimate of q , and this value is compared with that reported by Ralston and Tagami (1992). An accurate estimate of catchability is important in order to better estimate exploitable biomass for management purposes.

Methods

A total of five submersible dives were conducted in the main Hawaiian Islands, at two sites off leeward Oahu in February 1988 and three sites off the Kona coast of the Island of Hawaii in August 1988 (Table 1). The Oahu sites were selected for their proximity to port and because of previously-observed concentrations in the area of unidentified red shrimp at appropriate depths (400–900 m) for *Heterocarpus*. The three Kona sites were selected as extremes in *H. laevigatus* yield for the area during a trapping survey using pyramid traps conducted in March 1988 (see Tagami and Barrows (1988) and Ralston and Tagami (1992) for trap description and trapping methods). Catches of *H. laevigatus* were lowest for the Kona area (<1 kg/trap-night) at one of the sites and highest (>10 kg/trap-night) at the remaining two sites.

Visual censuses

All dives used the *Pisces V*, a three-man submersible that allowed simultaneous observations by two researchers through separate view ports with non-overlapping fields of view directed diagonally forward and down. A video camera continuously recorded the bottom throughout each dive as well. The same two researchers estimated shrimp abundance on all dives and independently reviewed the dive video tapes as a check on observer bias. On each survey, the submersible descended to depths of 480–920 m, then traveled to an arbitrary starting location at ~600–750 m depth. At this point, a baited container was placed on the bottom and observations of shrimp behavior in the presence of bait were recorded. After observing shrimp behavior for ~15 min, the submersible traveled a haphazard, rectangular track at a speed of ~2 knots along the contours within the zone of maximum shrimp abundance (defined below), returning to the baited container for retrieval at the end of the dive. At preselected time-intervals (5 or 10 min), the submersible settled to the bottom and counts of shrimp were taken by each observer in an independent quadrant filling the field of view. The estimated area of each quadrant was 10 m², which was calibrated by underwater observa-

Table 1
Locations of five study sites off the islands of Oahu and Hawaii and 1988 sampling dates.

Site no.	Location	Dive date	Trap date
Oahu			
1	21°19.3'N, 158°10.1'W	8 Feb.	13 Mar.
2	21°31.0'N, 158°16.8'W	9 Feb.	13 Mar.
Kona			
1	19°14.0'N, 155°54.9'W	23 Aug.	18 Mar.
2	19°20.7'N, 155°54.2'W	24 Aug.	18 Mar.
3	19°47.5'N, 156°07.8'W	25 Aug.	15 Mar.

tion of known dimensions with the submersible attached to its launch-and-retrieval vehicle. The minimum distance between observation sites was ~100 m. The number of observations of shrimp density varied between dives, for bottom time was dependent on battery power.

Bottom depth, temperature, and substrate type were recorded with each shrimp count. The substrate within each quadrant was categorized by composition and particle size of the major component. Substrate composition included coralline, volcanic, and mixed; particle size included sand, rock both small (<15 cm diameter) and large (>15 cm diameter), and pavement.

A χ^2 goodness-of-fit test using a Poisson distribution for the expected frequencies was conducted to determine whether *H. laevigatus* were concentrated or evenly distributed over the bottom at each dive site. Mean *H. laevigatus* density and 95% CI was calculated for each dive site based on a Poisson distribution,

$$CL = D_{(i)} \pm (1.96) \left(\frac{D_{(i)}}{n_{(i)}} \right)^{1/2},$$

where $D_{(i)}$ and $n_{(i)}$ are the mean density and number of observations for each dive site. Expected density values (De) for each site were calculated using trap landings for the site and the normalized catchability coefficient (q) reported by Ralston and Tagami (1992), using the following formula:

$$De_{(i)} = \frac{CPUE_{(i)}}{q}.$$

Confidence limits for the expected density values for each site could not be calculated, since variance cannot be computed for CPUE, based as it is on the catch of a single trap.

An analysis of variance (ANOVA) was performed to determine whether higher mean densities of *H. laevi-*

gatus could be attributed to different dive sites or bottom types and to determine whether there was observer bias. Independent variables for the ANOVA were dive site, substrate material, substrate particle size, and observer.

Comparisons of trap landings and density estimates

Trap catch rates were obtained in March 1988 from one pyramid shrimp trap set at each of the five dive sites and allowed to soak overnight (see Ralston and Tagami (1992) for details). Trap catches of *H. laevigatus* were regressed against mean densities obtained from visual counts for the five study sites, fitting a linear model with a zero intercept. The slope of this regression is an estimate of q , which was compared with that reported by Ralston and Tagami (1992).

Results

A total of 923 shrimp were captured in the 5 pyramid traps set at the study sites. Of these, 705 (76%) were *H. laevigatus* (Table 2), 217 were *H. ensifer*, and 1 was *Acanthephyra eximia*. During the scheduled observation periods on the submersible dives, a total of 494 shrimp were observed (194 total quadrant observations). Of these, only 95 (19%) were *H. laevigatus*, and the remainder consisted primarily of *Plesionika* sp., tentatively identified as *P. ensis*, and a few individuals of *P. alcocki*, *H. ensifer*, *A. eximia*, and *Gnathopausia longispina*. All *H. laevigatus* observed from the submersible appeared well within the size range of those captured in the traps, indicating that both stock assessment methods sample the same population.

Visual censuses

During our dives, the shrimp showed little reaction to the presence of the submersible or its lights. When the submersible came within a few inches of the shrimp, they swam a short distance avoiding collision. When the photoflash was used, the shrimp within a few feet of the submersible started, darting a distance of 1–4 cm. No other reactions to the submersible or its lights were observed. Several behavioral differences were noted between the various species observed.

A total of 94% (89 of 95) of the *H. laevigatus* observed during census periods were seen between 550 and 675 m, the depth range herein defined as the zone of maximum abundance. Individuals of *H. laevigatus* were observed at each dive site, but not necessarily during the scheduled census periods conducted within the zone of maximum abundance. Only counts taken within

Table 2

Trap catches, predicted densities, and mean observed densities with 95% CL of *Heterocarpus laevigatus* at five study sites off the islands of Oahu and Hawaii in 1988. N = the number of observations.

Dive site	Trap catch (n/trap)	Density (n/ha)		CL	N
		Predicted	Observed		
Oahu					
1	5	0.53	0	—	34
2	26	2.7	0	—	8
Kona					
1	0	0	200	(-680)-1080	10
2	376	40	1360	(-570)-3290	14
3	298	31	890	220-1560	76

this depth range were used in the analysis.

Heterocarpus laevigatus were observed as solitary individuals on the bottom, usually stationary but occasionally walking, and rarely swimming near the bottom. They showed little activity in the presence of a baited container and were not observed crawling over or entering it. Conversely, *H. ensifer* were found in groups near relief features (e.g., large sea anemones) at shallower (450–550 m) depths, either stationary on the bottom or swimming about 1 m above the bottom. They were very active in the presence of a baited container, aggregating quickly and crawling over and entering the container through the mesh and other holes. *Plesionika alcocki* usually were seen on the bottom, whereas *P. ensis* generally were seen hanging motionless in the water column ~1–2 m off the bottom. Each showed some activity around the baited container. *Acanthephyra eximia* and *G. longispina* were observed swimming 1–2 m off the bottom, but were not seen at the baited container.

Bottom temperature varied during the dives from a low of 3.9°C at 920 m to a high of 6.0°C at 480 m. The temperature range within the zone of maximum *H. laevigatus* abundance was 4.8–5.9°C.

Bottom type varied considerably among the sites. The bottom at the two Oahu sites was classified as coralline sand making up an even, featureless plain with a gradual (<20°) slope. The bottom at the three Kona coast sites was much steeper, generally about a 35–45° slope, but with some sections near vertical or even slightly undercut at the Kona site 3. At Kona site 1, the bottom was nearly uniformly composed of small (5–10 cm diameter), sharp-edged volcanic rocks and very little coralline material. Kona site 2 differed from site 1 in that the small volcanic rocks were more weathered and the substrate had a greater coralline component. Kona site 3 had many sandy areas, at

Table 3

Analysis of variance for *Heterocarpus laevis* density by dive, bottom type, and observer.

Source	df	SS	MS	F	P
Dive	4	31.25	7.81	6.87	0.0001
Substrate					
material	2	24.53	12.26	10.79	0.0001
particle size	3	5.96	2.98	2.62	0.0765
Observer	1	3.40	3.40	2.99	0.0859
Error	132	150.08	1.14	—	—
Corrected total	141	215.22	—	—	—

times covering the entire 10m² quadrant, as well as areas of exposed limestone often forming undercut cliffs, and areas of small weathered volcanic rocks.

The distribution of *H. laevis* over the bottom was evaluated in several ways. No significant values were found for the χ^2 goodness-of-fit tests ($P > 0.10$) of the density observations recorded at each dive site, suggesting that the shrimp were randomly distributed (in a Poisson manner) instead of clumped at each dive site. The mean and confidence intervals of *H. laevis* density observed at each dive site are presented in Table 2. Pooling data from all dive sites for the independent variables (dive site, substrate material, substrate particle size, and observer), only dive site and substrate material were significantly correlated with shrimp density (ANOVA, $P < 0.05$; Table 3). The distribution of residuals did not differ significantly from a normal distribution. Independent review of the dive video by each observer yielded complete agreement on *H. laevis* counts and substrate classification, indicating a lack of observer bias in shrimp density estimation and substrate associations.

Comparisons of trap landings and density estimates

Mean observed densities were regressed on trap catches for each dive site (Fig. 1) ($r^2 = 0.97$, $P = 0.0003$). The least-squares regression equation is

$$\text{CPUE}_i = 0.2896 (D_i), \quad (\text{SE } 0.02364).$$

An estimate of catchability is obtained directly from the value of the slope (0.2896 ha/trap-night) with a confidence interval calculated as 0.2144–0.3648/trap-night. This estimate of catchability is $< \frac{1}{30}$ th that reported by Ralston and Tagami (1992) and is reflected in the differences between observed and

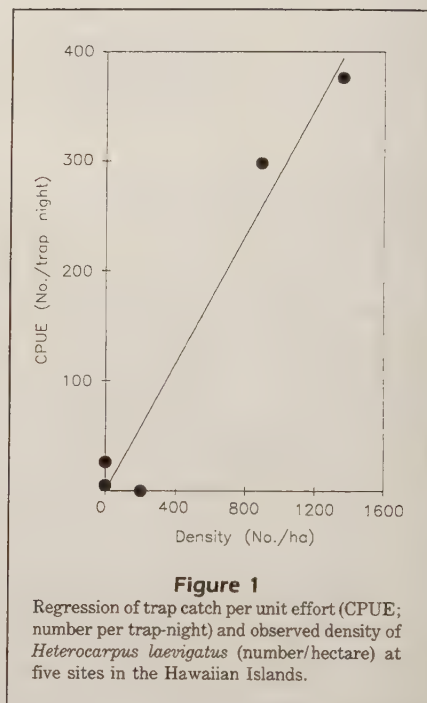


Figure 1

Regression of trap catch per unit effort (CPUE; number per trap-night) and observed density of *Heterocarpus laevis* (number/hectare) at five sites in the Hawaiian Islands.

expected *H. laevis* densities for Kona sites 2 and 3 (Table 2).

Discussion

Differences in behavior between *H. laevis* and *H. ensifer*, the two species with greatest commercial potential, may lead to some practical applications for fishermen. The high activity level noted for *H. ensifer* in the presence of a baited container has also been reported by Gooding et al. (1988) and Saunders and Hastie (1989). The rapid attraction and entry of this species into traps, even during daylight hours, indicate that a short soak time may be adequate for commercial harvesting. The lower activity level of *H. laevis* observed in our study and reported by Saunders and Hastie (1989) may indicate that a longer soak time is more appropriate for this species. If so, a small vessel with a limited number of traps could maximize total catch by making two short sets during daylight hours on *H. ensifer* grounds, followed by an overnight set on *H. laevis* grounds, assuming that suitable concentrations of both species are present within a reasonable proximity.

Previous observations of *H. ensifer* from a submersible found higher densities on flat, silty, sandy areas than over low-relief, rocky outcroppings (Gooding et al. 1988). Although statistical analysis of substrate associations were not conducted for *H. ensifer* in this study, we did observe a similar substrate association. *Heterocarpus ensifer* were abundant at the Oahu dive sites at depths (500–800 m), although this is deeper than their reported optimum range of 300–600 m (Gooding 1984). The substrate on these two dives was flat, coralline sand with few isolated, low-profile features (e.g., sea anemones, small rocks) around which the shrimp appeared to concentrate. No rocky outcroppings were observed on these dives. Very few *H. ensifer* were observed at the three Kona dive sites, where the bottom was steep and composed largely of rocky rubble with few sandy patches, though the dive depths again were deeper than the optimum range for this species.

The substrate associations of *H. laevigatus* appeared to differ from those of *H. ensifer*. Although the differences in substrate particle size were not significant, the ANOVA test revealed significantly higher densities on volcanic compared with coralline substrates (Table 3) with data from all dive sites pooled. The significant results for substrate type, however, must be viewed with caution because of the significance of dive site to *H. laevigatus* density and the unbalanced sample design. Not only were all substrate types not present on a single dive, but those types present were not found in equal proportions on any dive. Therefore, differences in density attributed to substrate type may actually be a reflection of differences related by some other factor to dive site. In particular, the Kona dive sites were largely volcanic, and the majority of the *H. laevigatus* observed were from Kona sites 2 and 3. Although Kona site 1 also was largely volcanic, the volcanic rocks differed from those observed at sites 2 and 3, in that the appearance was of a more recent rock slide (sharper edges vs. weathered). This apparent instability may be responsible for the low shrimp density observed at site 1. Other aspects of the bottom, such as slope, substrate complexity, stability, and current patterns may be of considerable importance and should be investigated in future work on the substrate associations of *H. laevigatus*.

With visual censusing techniques, there is always a concern regarding the reliability of abundance estimates. Various factors, including sampling techniques, species behavior, and physical conditions, can bias results (Colton and Alevizon 1981, Sale and Douglas 1981, Brock 1982, Ralston et al. 1986, Matlock et al. 1991). Some authors believe that density estimates based on direct visual surveys, though often much higher, are more reliable than those estimated from fishing gear catches (Uzmann et al. 1977, Powles and

Barans 1980, Kulbicki and Wantiez 1990). Individuals of the target species, *H. laevigatus*, were easily counted because they were in the open and reacted almost with indifference to the presence of the submersible, and because the low, uncomplicated relief at the study sites offered little opportunity for their concealment. Avoidance of the submersible by the shrimp seems unlikely. Observed densities were much greater than expected, yet these would be underestimates if avoidance occurred. We cannot discount the possibility of bias in our density estimates caused by attraction of shrimp to the baited container placed at the beginning of our dives. However, we observed no increased density gradient in the vicinity of the container, and density observations were taken well away from the container site (>100 m), presumably outside the drawing range of the bait, leading us to believe that bias due to this source was small.

Recalculation of exploitable biomass for the main Hawaiian Islands using Ralston and Tagami (1992) data and methods, but substituting the q value obtained in this study, would lead to a 33-fold increase in the estimate of exploitable biomass (~9000 t instead of 271 t). Just as Ralston and Tagami (1992) suggest that their estimate may be too low, we suggest that 9000 t may be unreasonably high, considering the preliminary nature of this estimate and the failure of the Hawaiian fishery that was at least partly due to drops in catch rates at annual yields of <200 t (Tagami and Barrows 1988). The acceptance of either of these estimates would drastically affect management decisions, and careful evaluation of these two values must be made. Contributions to the difference between the two estimates may be from three sources: actual differences in catchability for the two studies related to differences in time and study locations, error in our estimate of q , and error in the Ralston and Tagami (1992) estimate.

The estimation of q can be influenced by a variety of factors including currents, water turbidity and temperature, type of bait, soak time of fishing gear, and density of the target species (Morgan 1974, Richards and Schnute 1986, Miller 1990). For the two studies involved in this discussion, many of the potential sources of error were standardized. Both studies used the same traps, same bait, and same soak times. They did not, however, conduct studies at the same location or time, and the range of catch rates encountered differed for the two studies. In both studies it is assumed that catchability is constant for all catch rates and densities involved, but this may not be true, particularly between studies. Unfortunately, we are unable to evaluate the extent of the error involved from these sources.

The estimate of q presented in this study could also be biased. Sources of potential bias include lack of

representative catch rates for study sites, error in density estimation, incompatibility of CPUE and density estimates collected at different points in time, and the few data pairs involved. Not only were shrimp catches for each dive site based on a single trap-night of effort, but also traps generally were set at depths greater than the observed range of maximum abundance determined from our submersible observations (~750 m vs. 550–675 m). This results in no estimate of error for CPUE estimates at each site and no way to determine whether the traps were set within the range of maximum shrimp abundance at the time of trapping. If the traps were not set within this zone, yields at our sites may underrepresent relative shrimp abundance, leading to a lower-than-actual estimate of q . Another potential source of error in our q estimate is the accuracy of our density estimate. Confidence limits on our density estimates are quite broad, allowing for a fair degree of error. At many dive sites this problem is related to the few observations of density taken within the zone of maximum abundance. Additional problems in density estimation associated with the presence of bait in the water during the dives have already been addressed. The question of compatibility between data pairs of density estimates and CPUE values obtained at different points in time stems from possible changes in density or in q over time. Although trap catch rates in the Mariana Archipelago did not vary significantly on a seasonal basis (Polovina et al. 1985), suggesting that q does not vary seasonally, *H. laevis* may undergo temporal changes in depth range on either a diurnal or seasonal basis (King 1984, Dailey and Ralston 1986). If such movements do occur (the evidence is not strong) and depth range expands or contracts during these changes, densities observed during midday periods in February and August may differ from those occurring during trapping in March. Finally, although the fit is quite good, our estimate of q is based on only five data pairs covering limited values of CPUE and density.

The potential error in the Ralston and Tagami (1992) q estimate depends on the appropriateness of using their habitat area estimate in normalizing q and the validity of the assumption of constant catchability for all members of the population. These error sources are not necessarily greater than those discussed above, but are much easier to quantify. Even when an accurate estimate of biomass is obtained for a study site, calculation of a normalized q is dependent on the estimated habitat area of the study site. Estimated habitat area is apt to be larger when depth range is estimated from trap catches, as opposed to visual surveys, because of the ability of the traps to draw shrimp outside of their normal depth range. Recalculating the habitat area of the Ralston and Tagami study site using the observed

depth range (550–675 m) instead of the reported range (420–640 m) results in a reduction in area to 63% of the original value (748 ha instead of 1187 ha). Normalizing q with this reduced study-site area estimate gives an adjusted q value of 5.999 ha/trap-night (CI 2.6709–9.3271 ha/trap-night). The ratio of this adjusted value to the q obtained in the present study is 20.7 instead of the original 32.7. Ralston and Tagami (1992) discuss the effect on their q value of a large portion of the population not being susceptible to trap capture for the duration of the study period. They supply evidence that their original estimate of catchability may have been four times too high, resulting in a four-fold underestimation of exploitable biomass. Other authors have reported similar overestimates of catchability resulting from depletion studies (Morgan 1974, Morrissey 1975, Miller 1990). A further four-fold reduction of the Ralston and Tagami q value results in a ratio of 5.9 relative to our q value and only 1.8 for the extremes of the 95% CL (the minimum value for the Ralston and Tagami confidence interval compared with our maximum value). Coupling these quantifiable factors with the non-quantifiable factors discussed above could bring the two estimates of catchability into agreement.

Because of the importance of accurate estimates of exploitable biomass to the management process, it would be desirable to conduct a combined technique survey of the *H. laevis* resource. This should include direct visual density estimation with a trapping study conducted at the same time and place to obtain a reliable estimate of catchability and thereby exploitable biomass. Until that time, the expanded exploitable biomass estimate (1050 t) for the main Hawaiian Islands as presented by Ralston and Tagami (1992) should be accepted for management purposes as a reasonable, conservative approximation.

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Mitochondrial metabolism of cardiac and skeletal muscles from a fast (*Katsuwonus pelamis*) and a slow (*Cyprinus carpio*) fish

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Tuna cardiac (atrium, compact and spongy ventricle) and skeletal muscle (red and white) were compared with carp tissues to determine the importance of mitochondrial differences in supporting the high aerobic capacities in tuna. Mitochondria isolated from red muscle of both species oxidized each of the physiological fuels at similar rates per milligram of mitochondrial protein, when differences in assay temperature are considered. The highest rate of oxygen consumption by ventricle mitochondria was 2 times greater in tuna than carp. The maximal oxidation rates were 3–4 times higher in ventricle than red muscle in both species. Tuna tissues had as much as 30–80% more mitochondrial protein per gram of tissue than carp. Morphometrically this was manifested as extremely densely packed mitochondrial cristae, rather than increased mitochondrial volume densities. In general, higher aerobic capacities of tuna ventricle and red muscle are primarily attributable to greater tissue mass and, to a lesser extent, differences in the nature or quantity of mitochondria per gram of tissue. Unlike ventricle and red muscle, tissues with relatively low mitochondrial contents in carp (white muscle, atrium) demonstrated several-fold higher mitochondrial contents in tuna. Enzyme analyses of tissue and isolated mitochondria suggest a greater dependence of tuna tissues on fatty acids as fuels. Activities of carnitine palmitoyl transferase (CPT) per milligram of protein were 2–2.5 times higher in tuna red muscle and ventricle mitochondria than in carp mitochondria from the same tissues. Whole tissue activity ratios of hexokinase/CPT, which indicate the relative importance of glucose and fatty acid metabolism, were 5 times higher in carp spongy ventricle and 12 times higher in carp compact ventricle. These data suggest that muscle aerobic capacity can be increased at several levels: tissue mass, mitochondrial volume density, cristae surface density, and mitochondrial specific activity. Large differences observed between carp and tuna muscles are due to cumulative effects of several of these factors.

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Les muscles cardiaques (muscle de l'oreillette, muscles compacts et spongieux du ventricule) et les muscles squelettiques (rouges et blancs) du Thon à ventre rayé ont été comparés à des tissus de la Carpe afin de déterminer l'importance des différences mitochondriales qui donnent lieu aux capacités aérobies élevées chez les thons. Les mitochondries extraites de muscles rouges des deux espèces oxydent chacun des combustibles physiologiques aux mêmes taux par milligramme de protéine mitochondriale lorsqu'on tient compte des différences de température expérimentale. Le plus haut taux de consommation d'oxygène enregistré dans les mitochondries du ventricule était 2 fois plus élevé chez le thon que chez la carpe. Les taux d'oxydation maximaux étaient de 3 à 4 fois plus élevés dans le ventricule que dans le muscle rouge chez les deux espèces. Les tissus du thon contenaient jusqu'à 30–80% plus de protéines mitochondriales/g de tissu que ceux de la carpe. Morphométriquement, cela se manifestait par la présence de crêtes mitochondriales extrêmement serrées plutôt que par une augmentation de la densité du volume mitochondrial. En général, la capacité aérobie plus élevée du ventricule et du muscle rouge du thon est surtout attribuable à une masse tissulaire plus grande et, à un degré moindre, à des différences dans la nature ou la quantité de mitochondries/g de tissu. Contrairement aux muscles du ventricule et au muscle rouge, le muscle blanc et le muscle de l'oreillette ont un contenu mitochondrial relativement faible chez la carpe, alors qu'il ont un contenu plusieurs fois plus élevé de mitochondries chez le thon. Des analyses enzymatiques des tissus et des mitochondries isolées ont démontré l'existence d'une dépendance plus grande à l'égard des acides gras comme combustibles dans les tissus du thon. L'activité de la carnitine palmitoyl transférase (CPT)/mg protéine était de 2 à 2,5 fois plus élevée dans les mitochondries du muscle rouge et du ventricule du thon que dans ceux des mitochondries des mêmes tissus chez la carpe. Le rapport entre l'activité de l'hexokinase et celle de la CPT dans les tissus entiers, rapport qui indique l'importance relative du métabolisme du glucose et du métabolisme des acides gras, était 5 fois plus élevé dans le muscle spongieux du ventricule et 12 fois plus élevé dans le muscle compact du ventricule chez la carpe. Ces résultats indiquent que la capacité aérobie du muscle peut être augmentée par plusieurs facteurs: la masse tissulaire, la densité du volume mitochondrial, la densité de la surface des crêtes et l'activité mitochondriale spécifique. Les différences observées entre les muscles de la carpe et ceux du thon sont attribuables aux effets cumulatifs de plusieurs de ces facteurs.

[Traduit par la rédaction]

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Introduction

An important determinant of the maximal aerobic power output of a muscle is the rate at which its mitochondria can produce ATP. Modest increases in aerobic capacity are observed in individual muscles with endurance training. Much greater differences in muscle aerobic capacity are observed when comparisons are made between muscle types (i.e., red, white, cardiac) or between species. Such comparisons suggest that there are two general mechanisms by which increased aerobic ATP production capacities are achieved in muscle: (i) more tissue (i.e., increased mass of muscle per kilogram of body weight), and (ii) higher mitochondrial capacity per gram of tissue. This can theoretically be achieved both quantitatively and qualitatively. Higher mitochondrial volume density (V_m (mt, f)) packs more mitochondria into a given tissue volume. Qualitative differences in mitochondria make more effective use of the intracellular volume devoted to mitochondria. One type of qualitative difference is more closely packed inner membrane cristae, measured as square metres of cristae surface area per cubic centimetre of mitochondrial volume (S_v (im, m)). Because the protein content of mitochondrial inner membranes is extremely high (Sreer 1985), more closely packed cristae allow more mitochondrial membrane protein per cubic centimetre of mitochondrial volume. A second type of qualitative difference involves changes in the nature or efficiency of the mitochondrial enzymes, which would be manifested as an increased ATP production per milligram of mitochondrial protein.

Qualitative differences in mitochondria between high and low-performance tissues and species are not well established. It has been suggested as part of the symmorphosis hypothesis that individual mitochondria from mammalian skeletal muscles are fundamentally similar regardless of tissue aerobic capacity (Hoppeler and Lindstedt 1985). Similar oxygen consumption rates are indeed observed with *in vitro* mitochondrial preparations from red and white muscles of mammals (Pande and Blanchard 1971; Schwerzmann et al. 1989). There is evidence for relatively minor changes in the nature of the mitochondria in response to endurance training, in which not all mitochondrial enzymes increase to the same extent (see Holloszy and Coyle 1984). However, when isolated mitochondria from trained and control rats are compared, rates of oxidation of physiological substrates (per milligram of mitochondrial protein) are not affected by training (Davies et al. 1981).

Qualitative differences in mitochondria are more obvious when comparisons are broadened to include nonmammalian vertebrates. A series of studies by Else and Hulbert (Else and Hulbert 1981, 1983; Hulbert and Else 1989) demonstrated that mammalian mitochondria have more densely packed cristae than mitochondria from the same tissues of similarly sized reptiles. Differences in muscle mitochondrial capacities per milligram of mitochondrial protein have also been observed. Red muscle mitochondria from elasmobranchs (Moyes et al. 1990) demonstrate rates of oxygen consumption that are 2 times higher than mitochondria from red or white muscle of teleosts (Moyes et al. 1989). Heart mitochondria tend to show higher rates of oxygen consumption per milligram of protein than do skeletal muscle mitochondria (e.g., Krieger et al. 1980 vs. Palmer et al. 1977). Furthermore, two intracellular populations of mitochondria (subsarcolemmal, interfibrillar) appear to have different oxidative capacities in both skeletal muscle (Kreiger et al. 1980) and heart (Palmer et al. 1977).

Apart from questions of oxidative capacity, increased aerobic performance appears to be accompanied by a change in tissue

fuel preference. Part of the transition to higher aerobic work capacities induced by endurance training (Holloszy et al. 1985) or natural selection (Driedzic et al. 1987) appears to be a greater reliance on fatty acids. The extent to which these changes are facilitated by specialization of the individual mitochondria has not been thoroughly assessed. Relative rates of oxidation of pyruvate and palmitoyl carnitine do not change in mitochondria from endurance-trained rats (Davies et al. 1981). Training in fish increases tissue activities of β -hydroxyacyl-CoA dehydrogenase (HOAD) in both red and white muscle, with little change in other mitochondrial enzymes, suggesting a greater reliance on fatty acids (Johnston and Moon 1980a, 1980b).

In the present study we compare the oxidative properties of heart (atrium, spongy and compact ventricle) and skeletal muscle (red – slow oxidative and white – fast glycolytic) from the high performance species skipjack tuna (*Katsuwonus pelamis*) and a low performance species, the common carp (*Cyprinus carpio*). Our goal was to assess the relative importance of mitochondrial differences in determining the aerobic capacity of fish muscle.

Materials and methods

Animals

Skipjack tuna (*Katsuwonus pelamis*), were purchased from local commercial fishermen. Fish weighing from 1 to 3 kg and of undetermined sex were held for up to 4 days in 10 m diameter tanks supplied with continuously flowing seawater ($25 \pm 1^\circ\text{C}$) at the Kewalo Research Facility, National Marine Fisheries Service, Honolulu. Carp (*Cyprinus carpio*) weighing 1–2 kg and of both sexes were netted locally and held for up to 3 months in outdoor tanks supplied with continuously flowing fresh water ($10\text{--}15^\circ\text{C}$) at the Department of Zoology, University of British Columbia. Carp were fed trout chow twice weekly.

Mitochondrial isolation

Fish were netted, quickly stunned by a blow to the head, and decapitated. A 2-cm steak was taken from the tuna immediately posterior to the anus. Red and white muscle were collected from both sides of the vertebral column. Whole ventricles from a single tuna or 2–3 carp were used for isolated mitochondrial studies. Mitochondria were prepared as described previously (Moyes et al. 1989) with the following modifications. Initial centrifugations of 5 min at $1400 \times g$ (4°C) were used to sediment undispersed tissue. Mitochondria were collected and washed by 7-min centrifugations at $9000 \times g$ (4°C). Aliquots of resuspended pellet (4–8 mg protein/mL) were frozen immediately in liquid nitrogen for enzyme assays. Mitochondria were used within 1.5 h for the oxygen consumption experiments.

Mitochondrial oxygen consumption

Incubations of tuna and carp mitochondria were performed at 25 and 15°C , respectively, which correspond to acclimation temperature. Small volumes of mitochondrial suspensions (25 μL of tuna heart, 50 μL of tuna red muscle, 100 μL of carp heart) were added to 2 mL of incubation medium of the following composition: 140 mM KCl, 20 mM HEPES, 5 mM Na_2HPO_4 , and 0.5% bovine serum albumin, pH 7.3, at 20°C . Oxygen consumption rates were monitored by a YSI Clark-type electrode. Respiratory control ratios (RCR) were determined for each preparation by adding carbon substrates followed 4–6 min later by 0.5 mM ADP. The RCR is the ratio of the state 3 rate (+ADP) to the state 4 rate determined after all the ADP is phosphorylated. To determine oxidative rates, mitochondria were given 0.1 mM malate and 0.5 mM ADP, then incubated 1–3 min until oxygen consumption reached a low, linear rate. At this point, saturating amounts of substrates were added to the cuvettes to elicit the state 3 oxygen consumption rates².

²Rates of mitochondrial respiration are expressed per unit atomic oxygen, the substrate for the electron transport system. Tissue and animal respiration rates are expressed per unit molecular oxygen, by convention.

TABLE 1. Oxidation of various substrates by mitochondria from heart and skeletal muscle

	Tuna		Carp		
	Heart	Red muscle	Heart	Red muscle ^a	White muscle ^a
RCR	14.2±2.8 (6)	14.9±2.2 (6)	>20 (6)		
Malate	20±2 (6)	8±2 (7)	24±3 (6)	6±1	5±1
Pyruvate	403±41 (6)	106±12 (7)	146±5 (6)	55±7	52±7
Palmitoyl carnitine	178±29 (6)	104±12 (7)	103±4 (6)	54±6	31±4
Lauroyl carnitine	150±14 (6)	87±11 (6)	89±4 (6)	56±8	36±4
Octanoyl carnitine	83±4 (6)	50±6 (6)	49±4 (6)	45±9	18±2
Acetyl carnitine	87±10 (6)	36±4 (6)	91±3 (6)		
Acetoacetate	58±5 (5)	16±2 (3)		9±1	8±1
Glutamate	53±5 (4)	23±4 (4)		33±6	20±4

NOTE: Values are given as means ± SE, in nmol O/(min · mg mitochondrial protein). Values in parentheses are number of preparations. Tuna data were collected at 25°C, carp at 15°C. RCR, respiratory control ratio.

^aData are from Moyes et al. (1989).

Enzyme assays

Tissues for enzyme analyses were quickly collected, frozen in liquid nitrogen, and stored on dry ice. Atrium, compact ventricle, and spongy ventricle were separated prior to freezing. All assays were performed within 7 days of tissue collection. Tissue samples were weighed and added to 6 vol. (w/v) ice-cold homogenization medium (20 mM HEPES, pH 7.4, 1 mM EDTA, 0.1% Triton X-100). Homogenates were prepared by dicing, sonicating (1 burst of 10 s on Kontes sonifier), homogenizing (3 bursts of 10 s on Ultra-Turrax homogenizer), and sonicating (3 bursts of 10 s) the tissue. Particulate matter was sedimented by centrifugation (5 min at 9000 × *g*, 4°C). Mitochondrial suspensions were diluted with the same homogenization medium (1/9 v/v) and sonicated (3 bursts of 10 s). Activities lost in the sedimented pellet were not determined but are assumed to be minimal, as this extraction procedure routinely yields measurements of enzyme activity comparable to, or as much as 3 times higher than, values previously reported for these species (e.g., Guppy et al. 1979; Sidell et al. 1987).

Maximal enzyme activities were determined using a Perkin–Elmer Lambda 2 spectrophotometer interfaced with an IBM computer using PECSS (Perkin–Elmer Computerized Spectroscopy Software). The cuvette holder was thermostatted to 25°C for both species. All assays were performed in duplicate, as follows:

Citrate synthase (CS): 20 mM Tris-HCl (pH 8.0), 0.2 mM 5,5'-dithio-bis(2-nitrobenzoic acid) (DTNB), 0.3 mM acetyl-CoA, and 0.5 mM oxaloacetate. Oxaloacetate was omitted for the control assays. Control rates were typically <5% of the CS rate.

Carnitine palmitoyltransferase (CPT): 20 mM Tris-HCl (pH 8.0), 0.2 mM DTNB, 0.1 mM palmitoyl-CoA, and 5 mM L-carnitine. Carnitine was omitted for the control assays. CPT rates were typically 2–3 times greater than control rates.

Hexokinase (HK): 20 mM imidazole (pH 7.4), 1 mM ATP, 0.5 mM NADP⁺, 5 mM glucose, 5 mM MgCl₂, 5 mM dithiothreitol, and excess glucose-6-phosphate dehydrogenase. Glucose was omitted in control assays. The HK rate was typically 2–3 times greater than the control rate.

Mitochondrial ultrastructure

Morphometric measurements of mitochondrial volume density ($V_v(\text{mt}, \text{f})$) and cristae surface density ($S_v(\text{im}, \text{m})$) were done as described previously (Hoppele et al. 1981; Mathieu et al. 1981). Details on tissue preparation are found in Mathieu-Costello et al. (1992). We analyzed two randomly chosen blocks in red muscle and compact and spongy ventricle, and four blocks in white muscle. A total of 32 pictures (each sample of heart and red muscle) and 80 pictures (white muscle) were examined at a magnification of × 24 000 to estimate $V_v(\text{mt}, \text{f})$. The $S_v(\text{im}, \text{m})$ was estimated from pictures of mitochondria taken at random from 10 (red muscle, heart) to 40

(white muscle) fibers examined at a final magnification of × 220 000. We measured a total of 20 subsarcolemmal and 40 interfibrillar mitochondria in red muscle, 40 interfibrillar mitochondria in white muscle, and 20 and 40 interfibrillar mitochondria in spongy and compact portions of the ventricle, respectively.

Results

Mitochondrial oxidation

The results of the isolated mitochondrial studies are summarized in Table 1. In both species maximal oxygen consumption rates were several times higher in mitochondria from heart than in those from muscle: 4 times in tuna, 3 times in carp. In each of the tissues examined, pyruvate was oxidized at the highest rates among all substrates tested. Tuna red muscle mitochondria oxidized palmitoyl carnitine and pyruvate at similar rates, as did carp red muscle mitochondria. Heart mitochondria of both species oxidized palmitoyl carnitine at lower rates than pyruvate (55% lower in tuna, 30% lower in carp). This pattern of pyruvate preference over fatty acids also occurred in carp white muscle.

Comparisons of mitochondrial respiration rates between species are complicated by the differences in assay temperatures (25°C for tuna, 15°C for carp), which were chosen to mimic acclimation temperatures. Carp red muscle mitochondria demonstrate a Q_{10} of 1.5, using lauroyl carnitine as substrate (Moyes et al. 1988). It is not known if a similar Q_{10} is applicable for all substrates or if the rates would change in such a manner if the acclimation temperature was 25°C. For the purposes of this study a Q_{10} of 1.5 is assumed for all substrates, with the recognition that this may be an oversimplification. With these reservations in mind, it appears that carp and tuna mitochondria are similar in most respects within tissue types. Maximal oxygen consumption (pyruvate) by cardiac mitochondria is almost 2 times higher in tuna than carp, whereas red muscle mitochondria respire maximally at similar rates in each species. Acetyl carnitine oxidation by carp heart mitochondria is about 150% that of tuna. Glutamate oxidation by carp red muscle mitochondria is about twice that of tuna.

Tissue enzymes

A summary of tissue enzyme activities is presented in Table 2. Citrate synthase activity per gram wet weight is used as an index of mitochondrial capacity. Of all tissues examined, the highest activities were observed in tuna atrium. Within tuna

TABLE 2. Tissue activities of citrate synthase (CS), carnitine palmitoyltransferase (CPT), and hexokinase (HK)

	CS (U/g)	CPT (U/g)	CPT/CS (mU/U)	HK (U/g)	HK/CPT (U/U)
Tuna					
Atrium (7)	87.88±2.45	1.26±0.18	14±2	13.55±0.42	10.8±1.4
Compact (7)	63.37±4.15	2.52±0.26	40±3	6.66±0.68	2.6±0.20
Spongy (7)	74.58±5.76	2.51±0.25	35±6	8.10±0.78	3.2±0.29
Red muscle (7)	79.8±2.15	2.40±0.05	30±0.4	2.03±0.16	0.85±0.05
White muscle (7)	16.1±0.95	nd	—	1.06±0.1	—
Carp					
Atrium (6)	18.12±1.27	0.30±0.022	17±1	6.97±1.24	23.2±3.6
Compact (5)	29.60±1.88	0.34±0.012	12±1	10.45±1.12	30.7±4.0
Spongy (5)	43.32±6.35	0.78±0.042	21±5	11.07±0.54	14.2±1.3
Red muscle ^a (6)	49.00±4.4	0.71±0.06	14.5	0.55±0.06	0.77
White muscle ^a (5)	3.50±0.2	nd	—	nd	—

NOTE: Values are given as means ± SE, where 1 U/g is 1 μmol substrate used/(min · g). All enzymes were assayed at 25°C. nd, not detected; —, not determined.

^aData are from Moyes et al. (1989), except the HK data.

TABLE 3. Mitochondrial enzymes assayed in isolated mitochondria

	CS (U/mg)	CPT (U/mg)	Mitochondrial protein (mg/g)	$\dot{V}O_{2MAX}$ (μmol O ₂ /(min · g))
Tuna				
Heart (6)	1.94±0.16	0.030±0.002	35.0 ^a	7.0
Red muscle (6)	1.64±0.06	0.039±0.003	48.7	2.6
Carp				
Heart (6)	1.34±0.11	0.016±0.001	24.4	1.8 ^b
Red muscle ^c	1.80±0.16	0.015	27.2	0.75 ^b
White muscle ^c	1.13±0.08	0.004	3.09	0.081 ^b

NOTE: Values are given as means ± SE, where 1 U/mg is 1 μmol substrate converted/(min · mg mitochondrial protein). Enzymes were assayed at 25°C.

^aCalculated as (CS/g)/(CS/mg), weighted for the relative amounts of compact and spongy myocardium (carp, compact, 37% of total mass, Bass et al. 1973; skipjack tuna, 65.6%, Farrell et al. 1992).

^bEstimates of oxygen consumption rates for carp are at 15°C.

^cEnzyme data are from Moyes et al. (1989).

heart, CS activity is ranked atrium : spongy myocardium : compact myocardium (100:85:72). Within carp heart, CS activity is ranked spongy myocardium : compact myocardium : atrium (100:67:42). Comparing the two species, tuna CS activity is higher in all tissues examined (2.1× higher in compact myocardium, 1.8× in spongy myocardium, and 1.6× in red muscle but particularly in atrium and white muscle (4.5–5×).

CS activities, expressed as units per gram wet weight (Table 2) and units per milligram of mitochondrial protein (Table 3), allow the calculation of milligrams of mitochondrial protein per gram of tissue (Table 3). Tuna tissues have a higher mitochondrial protein content than those of comparable carp tissue (43% higher in heart, 80% in red muscle). The maximal ventricular oxygen consumption can be estimated from mitochondrial protein content (Table 3) and oxygen consumption per milligram of protein (Table 1). When the differences in assay temperature are considered, tuna tissues have 130–140% higher maximal oxygen consumption per gram than the corresponding carp tissues.

CPT activities were also higher in tuna tissues: atrium, 4.2×; compact, 7.4×; spongy, 3.2×; red muscle, 3.4×. Within tuna, CPT activities were similar in red muscle and compact and spongy ventricle, each being approximately twice

that of atrium. CPT activities in carp atrium and compact ventricle were each about half those in spongy ventricle and red muscle.

In oxidative muscles, HK/CPT ratios may reflect the fuel preferences of the tissue. Red muscle HK activities are several times lower than those in the heart tissues. In tuna and carp red muscle, HK activity is slightly lower than CPT activity, resulting in HK/CPT ratios less than unity. HK activity per gram is similar in the heart tissues of each species but, unlike red muscle, it is several times higher than CPT activity. HK/CPT in tuna ventricle is approximately 3, but in carp this ratio is 14 in spongy ventricle and 30 in compact ventricle.

Mitochondrial enzymes

Direct comparisons of mitochondrial enzymes (activity per milligram of mitochondrial protein) between species (Table 3) are possible because all enzymes were assayed at 25°C. No clear pattern emerges in CS activity per milligram of protein between tissues or species. Activities are marginally higher in heart than red muscle in tuna, but the reverse is seen in carp. Activities in tuna heart are slightly higher than those in carp heart. Activities are similar in red muscles of each species.

CPT activity is often used as an index of the capacity for fatty

TABLE 4. Tuna muscle mitochondrial ultrastructure

	Volume of mitochondria/ volume of fiber (%)		Surface area of inner mitochondrial membrane/ volume of mitochondria (m ² /cm ³)		Surface area of inner mitochondrial membrane/volume of fiber (m ² /cm ³)
	Subsarcolemmal mitochondria	Total mitochondria	Subsarcolemmal mitochondria	Interfibrillar mitochondria	
Heart					
Compact	1.7±0.1	25.4±1.0	—	57.88±1.57	14.70
Spongy	1.7±0.5	25.3±0.7	—	56.63±1.36	14.33
Red muscle	12.3±2.4	32.4±1.9	63.20±1.60	70.61±1.67	21.89
White muscle	0.3±0.2	2.5±0.3	—	31.32±1.66	0.78

acid utilization by a tissue. This study demonstrates that differences in CPT activity are not necessarily accompanied by differences in the maximal mitochondrial capacity to utilize fatty acids. CPT activity per milligram of protein is 2–2.5 times higher in tuna than in the same tissues in carp, but carp and tuna have similar tissue-specific oxidation rates for mitochondrial palmitoyl carnitine, when differences in assay temperature are considered. Although CPT activities (U per milligram of protein) were 30% higher in tuna red muscle than tuna ventricle (Table 3), mitochondria from heart oxidized palmitoyl carnitine at 70% greater rates than red muscle (Table 1). A similar situation occurs in carp, in which 2-fold greater palmitoyl carnitine oxidation rates in heart (Table 1) occurred despite similar CPT activities per milligram of protein (Table 3).

Tuna mitochondrial ultrastructure

Mitochondrial volume density ($V_v(\text{mt}, \text{f})$) and cristae surface density ($S_v(\text{im}, \text{m})$) determinations are summarized in Table 4. Tuna red muscle has a high $V_v(\text{mt}, \text{f})$, approximately 30 times higher than that of white muscle. In eight muscle samples from four fish, $V_v(\text{mt}, \text{f})$ ranged from 24 to 32% (Mathieu-Costello et al. 1992). Heart $V_v(\text{mt}, \text{f})$ is approximately 25% in both compact and spongy myocardium. Subsarcolemmal mitochondria comprised 35% of the total in red muscle but only 7% in the heart. In other red muscle samples, subsarcolemmal mitochondria comprised 17–40% of the total mitochondrial volume (Mathieu-Costello et al. 1992). $S_v(\text{im}, \text{m})$ in red muscle is higher than in tuna heart. The total mitochondrial cristae surface area per cubic centimetre of muscle in heart was 65% of the value in red muscle. A representative electron micrograph of interfibrillar mitochondria in red muscle is shown in Fig. 1. It is taken from one of the micrographs used for morphometry, i.e., it represents mitochondria selected by systematic random sampling.

Discussion

Aerobic capacity

There are two potential strategies to increase tissue aerobic capacity: (i) more aerobic tissue per kilogram of body mass or (ii) higher mitochondrial capacity per gram of tissue (morphometrically as increased $V_v(\text{mt}, \text{f})$ or $S_v(\text{im}, \text{m})$, metabolically as increased oxidation per milligram of protein or milligrams of mitochondrial protein per gram). When tuna and carp are compared, each of these strategies is used to some extent, and the relative importance of each depends on the tissue. In general, it appears that highly aerobic tissues (heart, red muscle) differ between species primarily in functional mass and to a lesser

extent in mitochondrial capacity per gram. In contrast, muscles that are mitochondria-poor in carp (white muscle, atrium) have mitochondrial capacities per gram that are several times higher.

The interspecies differences in red muscle mitochondrial properties are modest. Substrate oxidation rates per milligram of mitochondrial protein are similar between species, when differences in assay temperature are considered. Tuna red muscle, however, has about 80% more mitochondrial protein per gram of tissue than that of carp. As the $V_v(\text{mt}, \text{f})$ found in tuna red muscle (32%) is within the range found in other teleosts (25–38%, see Johnston 1981), the higher amount of mitochondrial protein per gram must be manifested as more densely packed cristae. The intracellular volume devoted to mitochondria in fish red muscle may approach the spatial limit allowed by cells that must also perform mechanical work (Weibel 1985, Hochachka 1987). Higher mitochondrial volume densities are observed in tissues such as the heater organ of billfish (Block 1986), which demonstrate high metabolic rates but do not perform mechanical work. If such a constraint exists in fish muscle, adaptations toward increased mitochondrial capacity per gram of tissue may necessarily involve increased $S_v(\text{im}, \text{m})$.

Cristae packing in tuna red muscle is exceptionally high for a vertebrate skeletal muscle. This avenue for increasing tissue aerobic capacity may also be limited in tuna red muscle. The value of 63–70 m²/cm³ (Table 4) reported for tuna red muscle $S_v(\text{im}, \text{m})$ is greater than the range reported for skeletal muscles of antarctic fish (25–37 m²/cm³, Archer and Johnston 1991) and a wide variety of mammals (20–40 m²/cm³, Hoppeller and Lindstedt 1985), hummingbird flight muscle (58 m²/cm³, Suarez et al. in press), and mammalian and reptilian hearts (38–66 m²/cm³, Else and Hulbert 1983). Srere (1985) calculated that a $S_v(\text{im}, \text{m})$ of 83 m²/cm³ is the maximum degree of cristae packing that will still allow enough matrix space for two average-sized Krebs cycle enzymes, each in contact with an opposing membrane. Thus it appears that the only structural strategy available to tuna to increase the total aerobic capacity of red muscle by several fold is to increase recruitable tissue mass.

Active, pelagic fish generally possess more red muscle than benthic or sluggish fish (Greer-Walker and Pull 1975). Higher aerobic capacity in fish skeletal muscle could also be achieved by utilizing white muscle during steady-state swimming. The limits to the use of white muscle at low swim speeds are based on innervation pattern and muscle ultrastructure (Johnston 1981). The fiber orientation necessary in white muscle to power burst exercise compromises its ability to function at lower

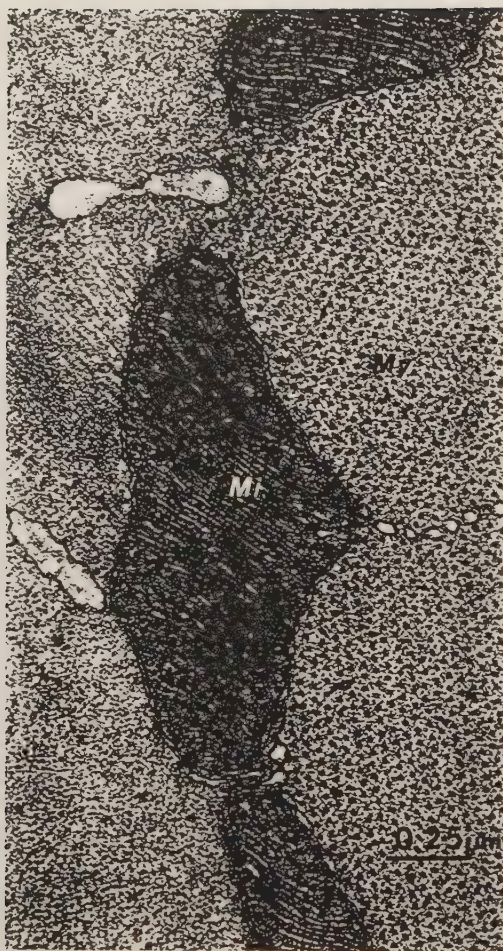


FIG. 1. Representative high-power electron micrograph of inter-fibrillar mitochondria in tuna red muscle, and used for morphometry. Note the high density of mitochondrial cristae. Mi, mitochondrion; My, myofibril.

swimming speeds (Rome et al. 1988). Electrophysiological studies suggest tuna white muscle is indeed recruited at sustainable swim speeds (Brill and Dizon 1979) as in several other fish species (Johnston 1981) but not in carp (Johnston et al. 1977). Previous metabolic and ultrastructural studies support an aerobic role for tuna white muscle (Guppy et al. 1979; Hulbert et al. 1979). It is highly vascularized and contains significant stores of intracellular lipid, a fuel that can only be used aerobically. In the present study, the mitochondrial content of tuna white muscle, based on CS activity per gram, was found to be 5 times higher than in carp, supporting the suggestion that tuna white muscle is used aerobically.

The major differences between species in myocardial oxidative capacity per kilogram of body weight are attributable to muscle mass. Mass alone affords tuna a 5-fold advantage in oxidative capacity per kilogram of body mass relative to carp

(4.0 vs. 0.76 g ventricle/kg). Skipjack tuna ventricular mass is higher than in most fish species (Poupa et al. 1981; Sidell et al. 1987), close to the range found in mammals (Poupa and Ostadal 1969; Driedzic et al. 1987). Higher mitochondrial capacity per gram of ventricle is also obvious in tuna, but this is of lesser quantitative importance than the increased ventricle mass. Tuna have more milligrams of mitochondrial protein per gram of ventricle (43% greater) and a 2-fold higher oxidative capacity per milligram of mitochondrial protein than carp. These three factors combine to give tuna a 14-fold greater myocardial oxidative capacity per kilogram of body mass, but much of this difference is due to ventricular mass.

Compared with tuna red muscle, ventricle has lower V_o (mt,f) and lower S_o (im,m). Although teleological, it is instructive to ask why tuna ventricle mitochondria are less packed than they could be, based on what is observed in red muscle. Large hearts are needed to obtain the high ventral aortic pressures observed in vivo (Brill and Bushnell 1991). However, power output per gram of ventricle in tuna is similar to that in other fish species (Brill and Bushnell 1992; Farrell et al. 1992), so selection for higher aerobic capacities per gram of tissue may have been minimal. As hemodynamic considerations probably determine atrial size, it is not surprising that the ratio of atrial mass to ventricular mass is similar in each species (15% in tuna, 18% in carp). As was the case with ventricle, the greater mass of tuna atrium (0.60 vs. 0.14 g atrium per kilogram of body mass in carp) provides a 4-fold higher aerobic capacity. However, tuna atrium also has an approximately 5-fold greater mitochondrial capacity per gram than carp atrium, based on CS activity per gram of tissue. The combined effect of higher mitochondrial capacity per gram and increased tissue mass provides tuna atrium with a 20-fold greater aerobic capacity per kilogram of body mass than carp atrium.

Studies using combined physiological, biochemical, and morphometric techniques suggest that mammalian skeletal muscle mitochondria at $\dot{V}O_{2\text{MAX}}$ in vivo may operate close to the maximal rates obtained with isolated mitochondria in vitro (Schwartzman et al. 1989). In the case of tuna heart mitochondria, the maximal oxygen consumption ($\dot{V}O_{2\text{MAX}}$) we predict from in vitro studies is close to that estimated to be required by the heart at whole animal $\dot{V}O_{2\text{MAX}}$. Myocardial oxygen consumption of trout swam at maximal sustained speed has been estimated to be 80 μL oxygen/(min $\cdot$ kg body mass), corresponding to 95 μL (or 4.0 μmol) oxygen/(min $\cdot$ g ventricle) (based on 15°C trout with 0.87 g ventricle/kg working at 7.2 mW/g, Graham and Farrell 1990). The maximal cardiac power output observed in skipjack tuna in vivo is 25 mW/kg body mass, determined on spinally blocked fish (Brill and Bushnell 1991). Using trout data relating oxygen consumption and power output (Graham and Farrell 1990), this work rate would require a myocardial oxygen consumption of 3.3 $\mu\text{mol}/(\text{min} \cdot \text{g ventricle})$ (based on 25°C tuna with 4 g ventricle/kg). Maximal mitochondrial capacity found in this study (7.0 $\mu\text{mol O}_2/(\text{min} \cdot \text{g})$) is more than 2 times greater than the maximal myocardial oxygen consumption rate observed in vivo. It has been suggested that the maximal cardiac output may be 1.5–2 times greater than that observed with spinally blocked tuna (Brill and Bushnell 1991). If this were the case, tissue maximal work rates could only be met aerobically by utilizing the entire mitochondrial capacity. However, in vivo, oxygen or substrate delivery, NADH/NAD⁺ ratio, or availability of ADP or phosphate could prevent ventricle mitochondria from reaching their maximal capacity. Given the high rates of lactate release

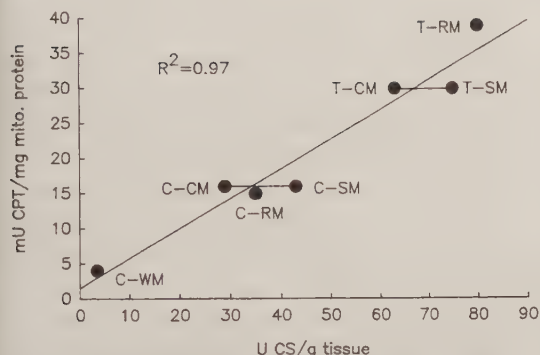


FIG. 2. Relationship between mitochondrial content (U citrate synthase per gram of tissue) and mitochondrial specific activity of carnitine palmitoyl transferase. A unit (U) represents the amount of enzyme required to convert $1 \mu\text{mol}$ of substrate to product in 1 min. C, carp; T, tuna; RM, red muscle; WM, white muscle; CM, compact myocardium; SM, spongy myocardium; mito., mitochondrial.

by isolated perfused tuna hearts (Farrell et al. 1992), it is likely that the heart's impressive glycolytic capacity would augment aerobic ATP production at such high power outputs.

Fuel preference

One of the consequences of training in mammals is greater reliance on fatty acids as fuels. Although a considerable part of this shift is related to fatty acid supply to the mitochondria, clear metabolic changes also occur at the muscle. Mitochondrial density in mammals increases with endurance training, and fatty acid catabolic enzymes increase in parallel, resulting in greater enzyme activity per gram of tissue (Holloszy et al. 1985). Endurance training of coalfish and brook trout causes increases in HOAD activities in red and particularly white muscle, suggesting that an increased capacity for fat oxidation also occurs in fish (Johnston and Moon 1980a, 1980b). Analogous to the intratissue changes that occur with endurance training is the increasing dependence on fatty acids as fuel in hearts of species with higher cardiac power outputs. When resting power output was plotted against enzyme activity, Driedzic et al. (1987) found that glycolytic enzymes (e.g., hexokinase) plateaued at low power demands, whereas the activity of enzymes catabolizing fatty acids (e.g., CPT) continued to increase. Along this line, the HK/CPT ratios may indicate the relative importance of exogenous glucose and fatty acids as fuels. The data from Driedzic et al. 1987 show that heart HK/CPT ratios of birds (pigeon 1.7) and mammals (rat 1.1) are considerably lower than those of reptiles (fence lizard 7.3, turtle 33), amphibians (grass frog 7.8, mudpuppy 21) and fish (trout 10.9, ocean pout 12, sea raven 22, hagfish 28). In this study, the HK/CPT ratio of carp ventricular tissue is as high as in other poikilotherms (14–30) but in tuna, the ratios are closer to those found in homeotherms (approximately 3), due primarily to higher CPT rates. Part of the differences in CPT activity per gram of tissue are due to a higher mitochondrial abundance in tuna, but there is also a difference in CPT activity per milligram of mitochondrial protein. Comparison of tissues with widely different aerobic capacities, from carp white muscle through to tuna ventricle, reveals a 10-fold difference in CPT activity per milligram of mitochondrial protein that correlates with the mitochondrial content of the tissue (Fig. 2). Higher

CPT specific activity does not necessarily result in greater rates of fatty acyl carnitine oxidation with isolated mitochondria in vitro (see the Mitochondrial enzymes section in the Results and also Palmer et al. 1977). The maximal mitochondrial capacities for palmitoyl carnitine oxidation rates utilize only a fraction of the measured CPT activity. For instance, in situ activity of 0.01 U CPT/mg mitochondrial protein can provide enough fatty acid substrate to result in an oxygen consumption of 460 nmol O ($\text{min} \cdot \text{mg}$ mitochondrial protein), well beyond the maximal rates observed in vitro. Even this may be an underestimate, as the activity of CPT in the direction required for palmitoyl carnitine oxidation is approximately 9 times greater than that in the direction which is assayed by the DTNB method (Palmer et al. 1977). It is likely that the higher CPT activities confer kinetic advantages to favour fatty acid utilization. Taken together, these data support the general hypothesis that more aerobic tissues rely more on fatty acids than glucose as fuel.

Previous calculations suggest that tuna cardiac mitochondrial capacity is similar to that which would be required at whole animal $\dot{V}\text{O}_{2\text{MAX}}$. If this mitochondrial capacity were realized in vivo, ventricular aerobic power output could reach 53 mW/kg body mass (14 mW/g ventricle) with pyruvate (from lactate, glucose) as substrate. However, a maximum of only 24 mW/kg (6 mW/g ventricle) could be generated with fatty acids as primary fuel. It should be noted that this fat-oxidizing capacity is sufficient to support the highest cardiac outputs measured in vivo (Brill and Bushnell 1991). This difference is due to the 2-fold mitochondrial fuel preference of pyruvate over fatty acids. As the enzyme analyses suggest fatty acids are relatively more important in tuna ventricle, the fuel preference of these mitochondria for pyruvate over fatty acids may reflect the capacity to use lactate as a fuel for heart metabolism. Lactate produced in tuna white muscle during exercise can reach 80–100 $\mu\text{mol/g}$ (Guppy and Hochachka 1978) and appears to be partly released from the tissue postexercise (Arthur et al. 1992). Lactate release following exercise may occur in channel catfish (Cameron and Cech 1990) but not in salmon or flounder (Milligan and McDonald 1988). Arthur et al. (1992) found that lactate concentration in tuna blood did not fall below 10 mM even when the white muscle lactate appeared to have recovered. Given the high rate of mitochondrial pyruvate oxidation relative to fat, it is tempting to speculate that fat may be used to fuel myocardial metabolism at low cruising speeds, whereas lactate may be used during or following high-intensity exercise, when the metabolic rate is high, blood lactate is elevated, and increased cardiac outputs are required.

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The Weddell–Scotia marginal ice zone: Physical oceanographic conditions, geographical and seasonal variability

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ABSTRACT

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Physical oceanographic conditions were measured in the Weddell and Scotia Sea marginal ice zones (MIZ's) during 1983, 1986 and 1988. The field work encompassed spring, autumn and mid-winter periods and included retreating, advancing and steady-state ice edges. Observed upper ocean structures, which typify MIZ's and reflect input of low salinity water from melting ice, included low salinity upper layers, lenses and fronts. An upper mixed layer was always present and was generally more fully developed in autumn and winter than at other times of year. Conditions in the deeper waters reflected regional oceanographic processes and significant differences were present between the Weddell and Scotia seas. Weddell Sea Water is a major source of water for the southern Scotia Sea, however, the upper Scotia Sea was dominated by warmer, less saline waters from Drake Passage. The colder, denser Weddell water appeared to have mixed isopycnally with deeper water in the Scotia Sea, present there at depths exceeding 500 m.

The Scotia Sea was dominated by strong gradients and energetic mesoscale features, with currents exceeding 50 cm/s. The northwestern Weddell Sea had, in contrast, current speeds well below about 5 cm/s and small to negligible lateral water property gradients. Our observations suggest that the Weddell western boundary current was weaker than has been estimated in the past. In addition, we found scant evidence of deep winter convection in the Scotia Sea, a process which has been hypothesized in the past to contribute to deep water formation. No evidence was found during winter 1988 in the Scotia Sea of the modified water known as Weddell–Scotia Confluence water.

Background

Introduction

The Weddell and Scotia seas (Figs. 1 and 2) are oceanographically continuous, linked by a broad, deep northward flow from the northwestern Weddell Sea into the southern Scotia Sea. The sea ice cover forms, also, a seasonally varying continuum between the two regions and in winter extends from the Weddell through the southern

Scotia Sea. Despite these continuous features, however, the Weddell and Scotia seas differ greatly in both their water mass structures and their energetics. This paper summarizes and integrates selected physical oceanographic results from the AMERIEZ Program (Smith and Garrison, 1990) and uses these results to illustrate contrasts between the Weddell and Scotia seas. The material herein is intended, also, as background for the interdisciplinary AMERIEZ papers presented elsewhere in this volume. Our

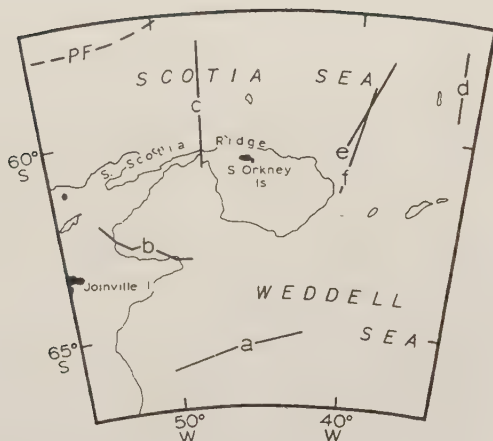


Fig. 1. Geographical location of the study region and of features referred to in the text. Lines *a-f* indicate locations of transects shown in Figs. 4-9 (see also Fig. 2). Dashed line *PF* indicates typical location for the Polar Front. Thin line indicates the 2 km bottom contour.

discussion will be limited to conditions shallower than 1500 m, the maximum sampling depths for the AMERIEZ program.

The oceanographic context

The western Weddell Sea can be characterized as a region of deep, sluggish northward flow which is the westernmost limb of the wind-driven, basinwide cyclonic Weddell Gyre (e.g. Gordon et al., 1978; Deacon, 1979; Gordon et al., 1981). The gyre-associated flow is predominantly barotropic, consistent with the weak lateral and vertical gradients in water properties; geopotential surface heights above the 1000 db level computed from historical data show only very weak baroclinic upper layer currents (Gordon et al., 1978). Total northward transport in the western Weddell is uncertain. Carmack and Foster (1975) derived a

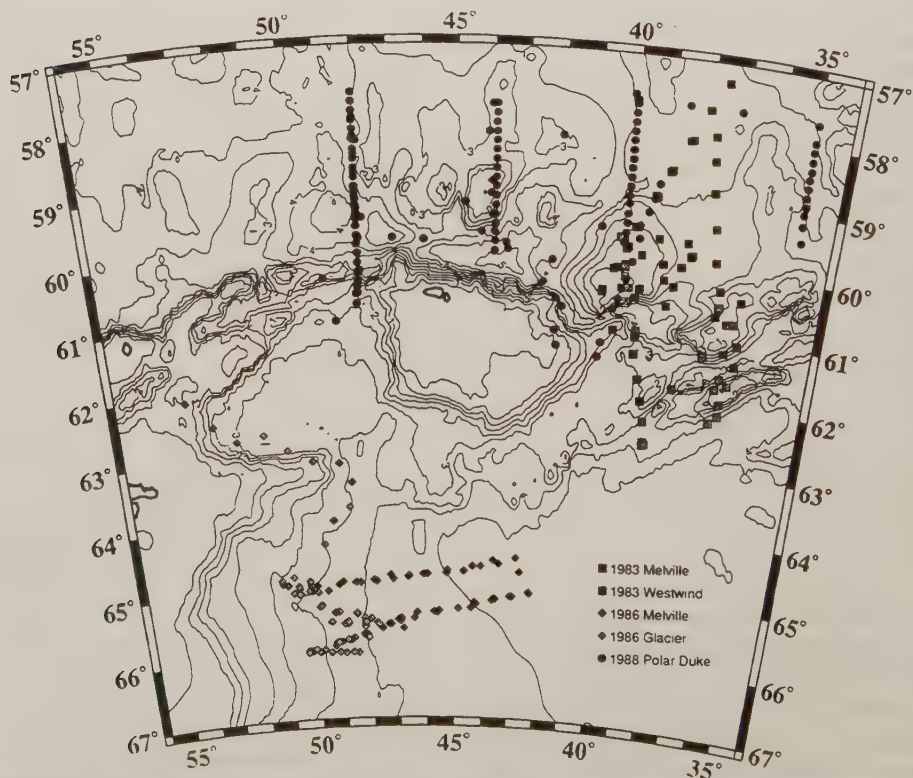


Fig. 2. Positions of CTD casts taken during the 1983, 1986 and 1988 AMERIEZ field programs. Bottom contours are labeled in km.

total gyre transport of $97 \times 10^6 \text{ m}^3/\text{s}$, however, their value was based upon a relatively small number of short-term current observations. Gordon et al. (1981) postulated a northward transport in the western Weddell of $76 \times 10^6 \text{ m}^3/\text{s}$ using closure of a wind-driven gyre. They also predicted vertically integrated current speeds of 8 cm/s and a western boundary current width of 225 km at 65°S. Observed mean northward ice drift speeds in the range of 5–10 cm/s (Ackley, 1979) are consistent with the above estimates of current speed.

The upper 1500 m of the Weddell Sea can be divided into three water masses (Carmack, 1977). Uppermost is the Weddell Surface Water, which varies seasonally in temperature and salinity due to warming and ice melting, cooling and freezing. This layer is underlain by a very sharp salinity-controlled pycnocline. Beneath this lies the Weddell Winter Water, which represents a remnant of the preceding winter's cold, convective layer. The Weddell Warm Water underlies the Winter Water. This layer contains the main thermocline between about 100–200 m and has a temperature maximum at 300–500 m. Beneath the sharp pycnocline, which spans a density range of order 0.5 sigma- t units, the vertical density gradient is extremely small. Likewise, lateral gradients in temperature, salinity and density are small. Mesoscale structures, which are common in temperate oceans and even over large areas of the Arctic Ocean, have not been observed in the northwestern central Weddell Sea (Muench, 1990).

In sharp contrast, the southern Scotia Sea is dominated by strong vertical and lateral gradients, many associated with mesoscale eddies and frontal structures (see e.g. Foster and Middleton, 1984). This very complex hydrographic field reflects the presence of water masses which originate in the Bellingshausen Sea, in the Weddell Sea, from Bransfield Strait and from the Antarctic Circumpolar Current. Scotia Sea Water is comprised primarily of a mixture of Bellingshausen Sea and Antarctic Circumpolar Current Water, and is readily identifiable in the southern Scotia Sea by subsurface temperature maxima at 400–500 m which can exceed 2–3°C. Weddell Sea Water enters the southern Scotia Sea from the

northwestern Weddell Sea over the South Scotia Ridge, through the gaps west and east of the South Orkney Islands. The transitional region in which Weddell and Scotia Sea waters converge and mix is called the Weddell–Scotia Confluence (WSC). Descriptions of the southern Scotia Sea, based primarily upon summer data and with general emphases on the WSC, have been provided by numerous authors but in the greatest detail by Deacon and Moorey (1975), Deacon and Foster (1977), Gordon et al. (1977) and Patterson and Sievers (1980).

The Weddell Sea water column is dominated by vertical processes, whereas the Scotia Sea is dominated by lateral processes. In the Weddell Sea, currents and lateral property gradients are small and the distributions of temperature, salinity and energy are strongly influenced by such vertical processes as double diffusion, cabelling, free convection due to brine rejection from freezing ice, and turbulence due to winds, ice drift and internal wave breaking (see, e.g., Foster and Carmack, 1976; Muench et al., 1990a). Currents and lateral property gradients in the Scotia Sea are large and the distributions of temperature, salinity and energy are controlled primarily by lateral advection and isopycnal mixing (Muench et al., 1990b).

The Weddell–Scotia Sea region is subject to a seasonally varying pack ice cover (Zwally et al., 1983; Comiso and Zwally, 1989) (Fig. 3). In summer, this ice is restricted to the westernmost Weddell sea. In winter, it extends throughout the Weddell Sea and northward for several hundred km into the southern Scotia Sea.

Field program

The AMERIEZ data were collected during field programs in the southern Scotia Sea during November 1983 and June–August 1988 and from the Weddell Sea during March 1986 (Figs. 1 and 2). Each of these programs was focussed on the MIZ. Each used different platforms and instrumentation and will therefore be summarized separately below.

Sampling during the 1983 program was carried out from the *R/V Melville*, which operated in the

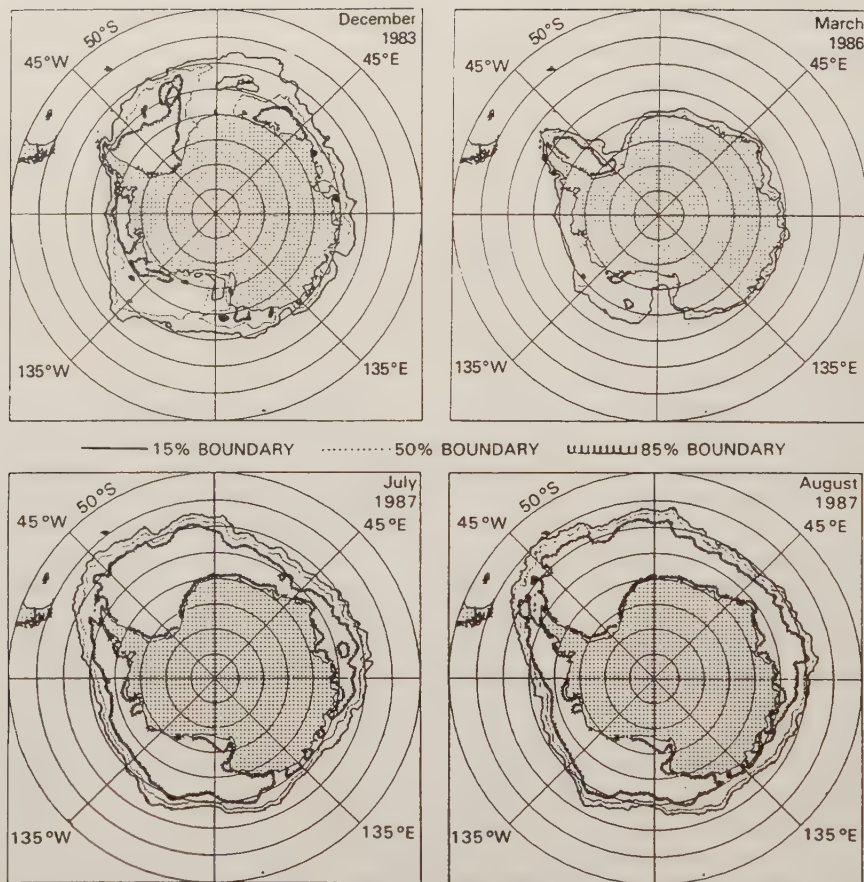


Fig. 3. Extent of sea ice at approximate mid-points of the 1983 and 1986 field programs, and ice extent for July–August 1987 showing ice extent which is typical for winter, from Comiso and Zwally (1989). Ice extent during the winter 1988 field program is not shown, but was similar to that shown here for July–August 1987.

open water and from the USCGC (United States Coast Guard Cutter) *Westwind* operating in the pack ice. Temperature and salinity observations were made from both vessels using vertically profiling conductivity/temperature/depth (CTD) systems. A Neil Brown Mark III CTD system was used on the *Melville* and an Ocean Data Equipment model 302 internally recording CTD on the *Westwind*. Standard CTD calibration practices were followed, using water samples collected during the cruise and calibration data obtained in the laboratory. Details are provided in Nelson et al. (1987).

Sampling during the 1986 program was carried out using Neil Brown Mark III CTD systems operated from two vessels; R/V *Melville* and USCGC *Glacier*. Both systems were calibrated prior to and following the cruise and standard calibration practices were followed during the cruise. *Melville* sampled seaward of the ice edge, and *Glacier* carried out sampling in the ice. Details of the cruise, instruments used, calibration and initial data analyses are provided in Husby and Muench (1988).

The June–August 1988 program was carried out during two sequential legs from the ice-

strengthened vessel R/V *Polar Duke*. Temperature and salinity measurements were obtained using a SeaBird model SBE 9/11 CTD system which was calibrated prior to and following the field program. Details for this winter field program are provided in Muench et al. (1990b).

Sea-ice distributions are provided for the 1983 and 1986 cruise periods in Comiso and Zwally (1989). Ice cover data for the 1988 cruises was provided in the form of unpublished images showing geographical ice cover and concentration data by J. Comiso (NASA/GSFC, 1990 pers. commun.). Ice extent during the 1983 and 1986 programs, and representative for the 1988 program, is shown in Fig. 3.

Results

Description of the temperature, salinity and density fields

Regional differences in temperature, salinity and density distributions are illustrated here through a sequence of transects, each approximately normal to and bracketing the MIZ, beginning in the northwestern Weddell Sea and progressing northward and eastward into the Scotia Sea (Figs. 4–7).

In the northwestern Weddell Sea, the distributions of T , S and density were characterized by lateral near-uniformity. A transect along about 65.5°S across the MIZ showed generally small lateral gradients and no mesoscale features (Fig.

4). The only significant MIZ-associated structure was a low-salinity layer which underlay the ice edge, was confined to the upper mixed layer, and was probably a remnant of ice melt from the directly preceding summer (not shown in figure, but documented in Nelson et al., 1989). The Winter Water ($T < 0^\circ\text{C}$) and Warm Water ($T > 0.4^\circ\text{C}$) layers were present. There was a general increase in upper-layer temperature toward the east, away from the ice.

A southeast–northwest transect farther north extended onto the continental slope and crossed the major outflow of water via the Weddell's western boundary current (Fig. 5). The Weddell Warm Water core was clearly evident ($T > 0.4^\circ\text{C}$), and deepened somewhat toward the continental margin. A cold, saline core ($S > 34.71$ ppt at about 800 m, decreasing to less than 34.70 ppt at 1500 m, where temperatures had decreased to less than -0.2°C) was present in the western half of the transect over the continental slope. This feature may have been cold, dense shelf water, flowing northward along the continental slope, as discussed for example by Foldvik et al. (1985). The weakly sloping isopycnals indicated that this water was denser than that farther offshore, but did not suggest that significant baroclinic flow was present. In the absence of direct current observations, quantitative statements concerning the currents here are not possible.

The next transect to the north falls fully in the southern Scotia Sea (Fig. 6) and demonstrates clearly the dramatic increase in water column

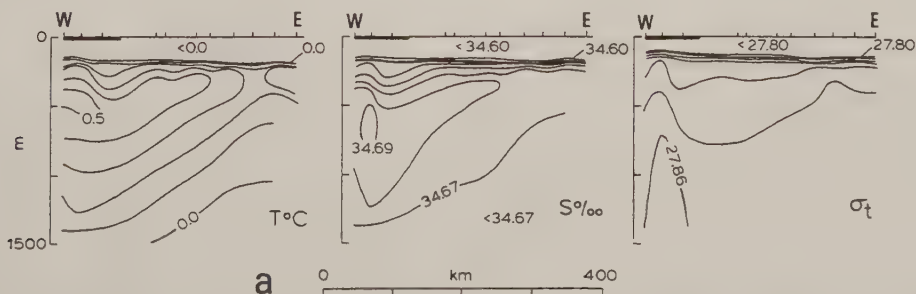


Fig. 4. Distributions of T , S and density (as σ_t) along southernmost (about 65.5°S) zonal March 1986 Weddell Sea CTD transect *a* (from Husby and Muench, 1988). Upper layer contours have been omitted for clarity. Bold dark line at the sea surface on this and the following three figures indicates presence of an ice cover. Tick marks at surface on this and subsequent transects indicate station locations. Location is shown on Figs. 1 and 2.

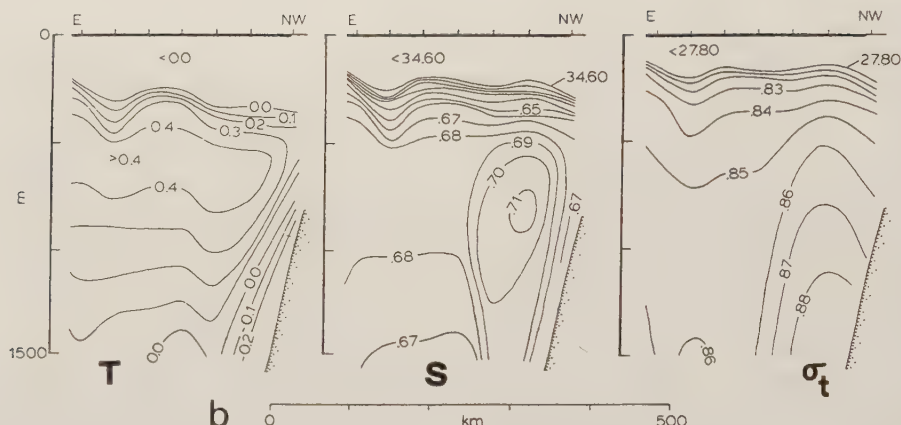


Fig. 5. Distributions of T , S and density (as σ_t) along March 1986 CTD transect b extending southeast–northwest, roughly coincident with the northwestern Weddell Sea continental slope, from about 63.5°S – 48.5°W to 62°S – 54°W (from Husby and Muench, 1988). Upper layer contours have been omitted for clarity. Location is shown on Figs. 1 and 2.

structure which occurs when the northward-flowing waters from the Weddell Sea converge with the eastward flow from Bransfield Strait and Drake Passage. The warm ($> 2^\circ\text{C}$) waters at 400–500 m in the northern part of the transect are derived from the Polar Front (Muench et al., 1990b). Small scale vertical structures suggest that interleaving was occurring across frontal regions. Temperatures increased throughout the water column toward the north, though there were alternating warm and cold features so that the increase was not monotonic.

The final transect was situated about 750 km farther east in the southern Scotia Sea, or downstream relative to the mean currents (Fig. 7). As farther west, warm deep water reflected the influence of the Polar Front and temperatures generally increased toward the north throughout the water column. While the structure was still complex relative to the northwestern Weddell Sea, it was less complex than farther west in the Scotia Sea. This reflects the decrease in gradients, through lateral mixing processes, during eastward flow from the origin of many of these features farther west where the currents first converge. Persistence of mesoscale features throughout the southern Scotia Sea study area was consistent

with Foster and Middleton's (1984) earlier results.

Finally, a limited seasonal intercomparison is possible in the southern Scotia Sea where there was partial spatial coincidence between meridional transects occupied approximately along 40°W during spring 1983 and winter 1988 (Figs. 8 and 9). This comparison suggests that virtually all of the seasonal variability is confined to the uppermost part of the water column. A thermal frontal structure, much more pronounced below the upper mixed layer than within it, was present about $3/4$ of the distance from the southern end of the transect both in 1983 and 1988. Temporal variability on a scale of weeks was as large as the interannual variation observed between 1983 and 1988.

Densities (σ_t) in the Weddell Sea were greater than 27.80 below the Weddell Surface Water layer. In the Scotia sea, waters of this density were found from 350 m (Fig. 7) to deeper than 1500 m (Fig. 6). Upper layer water from the northwestern Weddell Sea will mix with deeper water in the Scotia Sea. Water from the Weddell Warm Water layer, having a density of 27.84–27.85, will occur below the 1500 m maximum sampling depth over much of the southern Scotia

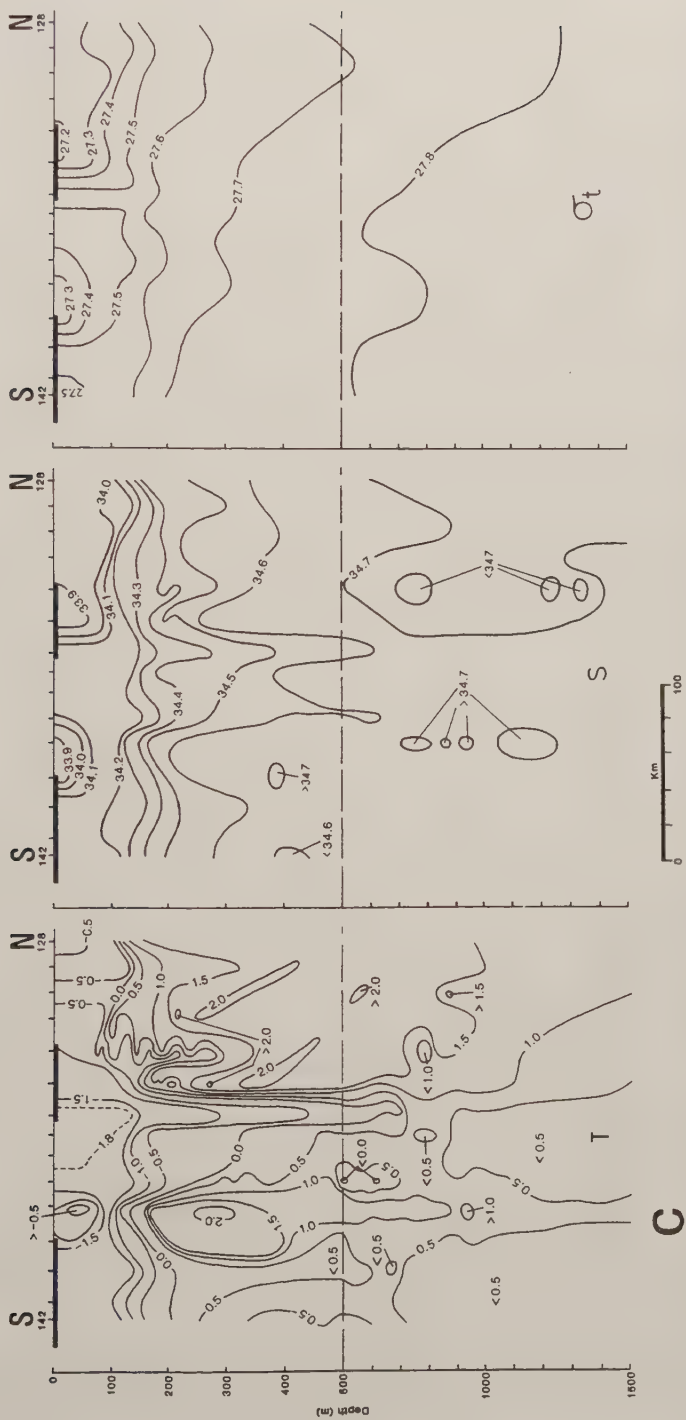


Fig. 6. Distributions of T , S and density (as σ_t) along westernmost (about 48°W) meridional August 1988 southern Scotia Sea transect c (from Muench et al., 1990b). Note that the depth scale is split at 500 m and that the scales and contour intervals are different than for Figs. 4 and 5. Location is shown on Figs. 1 and 2.

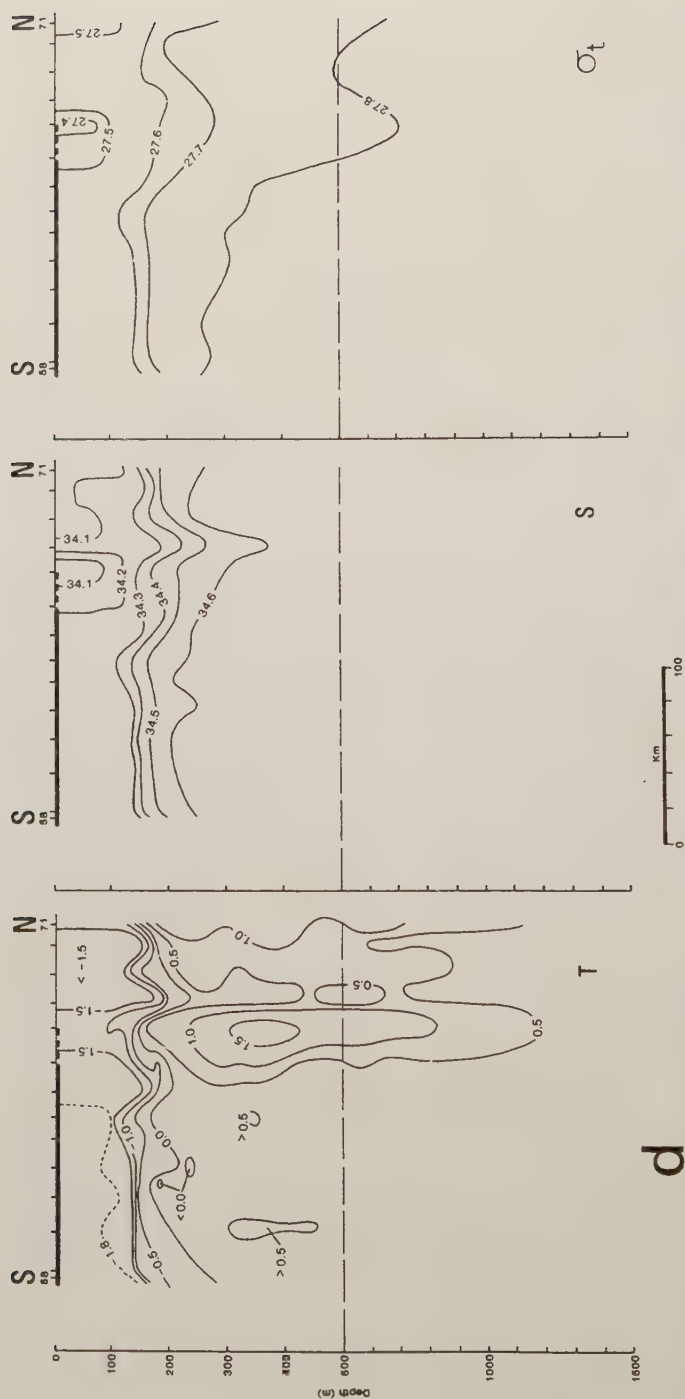


Fig. 7. Distributions of T , S and density (as σ_t) along easternmost (about 35°W) meridional July 1988 southern Scotia Sea transect d (from Muench et al., 1990b). Horizontal and vertical scales, and contour intervals, are as for Fig. 6. Location is shown on Figs. 1 and 2.

Sea region. This tendency for upper layer Weddell Sea waters to mix along isopycnal surfaces during northward movement and mix with deeper Scotia Sea waters was recognized by Deacon and Foster (1977).

The regional circulation

No direct observations of currents were made in the northwestern Weddell Sea, a region which has been characterized as having very weak mean currents. The data obtained during autumn 1986 were used by Husby and Muench (1988) to construct a dynamic topography of the sea surface relative to the 1500 db pressure surface. The resulting dynamic relief, and inferred baroclinic circulation, implied that a virtually insignificant surface baroclinic current (> 1 cm/s) was present, consistent with previously published results. This current was northward, following the general trend of the late summer ice edge up to a location east of Joinville Island. At this point, the

surface flow appeared to turn westward, again following the ice edge. This baroclinic flow pattern is contrary to the northeastward flow which we might expect to find in this region, and might reflect a summer accumulation of meltwater in the upper ocean layers beneath the ice edge. The surface dynamic topography relative to 500 db showed a similar pattern with about half as much relief. The baroclinic field was weak (< 1 cm/s) relative to the estimated 8 cm/s northward barotropic current speed (Gordon et al., 1981) and the upper layer baroclinic currents probably do not significantly impact the total regional flow in the northwestern Weddell Sea.

Direct evidence of northward surface flow was provided during the months following the 1986 field program by the drift of an ice floe which had been instrumented with an Argos drift buoy. The drift of this floe was qualitatively consistent with previous ice drifts shown by Ackley (1979). It remained essentially motionless from March–April 1986 and accelerated northward in late

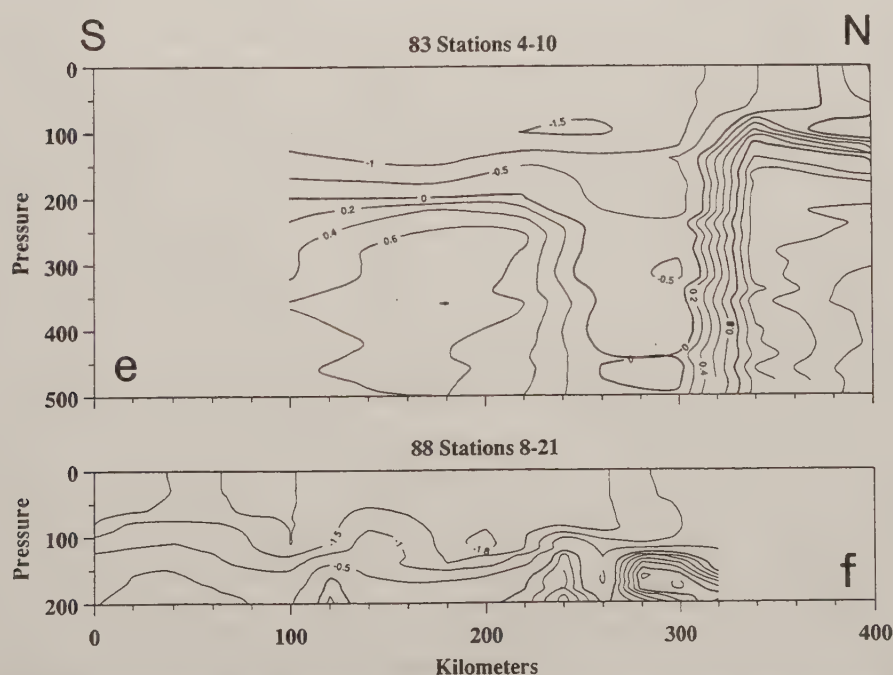


Fig. 8. November 1983 distribution of T along transect e at about 40°W in the southern Scotia Sea (upper) and June 1988 distributions along transect f (lower) which partially overlaps the 1983 transect. Locations are shown on Figures 1 and 2.

April with speeds of 5–10 cm/s, finally veering from northward to eastward in the southern Scotia Sea as it was entrained into the eastward regional current there and providing clear evidence of flow continuity from the Weddell into the Scotia Sea. Though we have no direct observations of surface winds, it is probable that the initial northward acceleration in April was due to south winds. It should be noted here that ice floe drift data are useful qualitative drift indicators, but caution must be exercised when extrapolating their drift to the underlying water because the ice is subject to surface wind and internal ice stresses as well as responding to surface currents.

Surface currents were measured in the southern Scotia Sea during winter 1988 by deploying near surface, drogued, Argos-tracked drift buoys at the upstream (western) end of the study area (Muench et al., 1990b). These drifters documented maximum surface current speeds exceeding 50 cm/s in a cyclonic mesoscale eddy, and general eastward currents in the northern part of

the study region were of order 10 cm/s, in contrast to the much slower currents to the south-west in the Weddell Sea.

In addition to the drogued drifters, a single-ice-floe drift measurement was obtained from the Scotia Sea during winter 1988 by deploying an Argos buoy on an ice floe west of the South Orkney Islands (Muench et al., 1990b). There was little motion in the region west of the South Orkneys. By August, the floe had moved northward sufficiently, possibly in response to south winds, that it was entrained into the eastward regional flow.

Muench et al. (1990b) constructed a dynamic topography of the sea surface relative to the 1500 db pressure level for the 'Scotia Sea using the winter 1988 data (the spring 1983 data were too limited in coverage to allow construction of a reasonably complete topography). The resultant topography documented strong eastward baroclinic flow in the northern half of the study area, the eddy in which the drifter was entrained, and

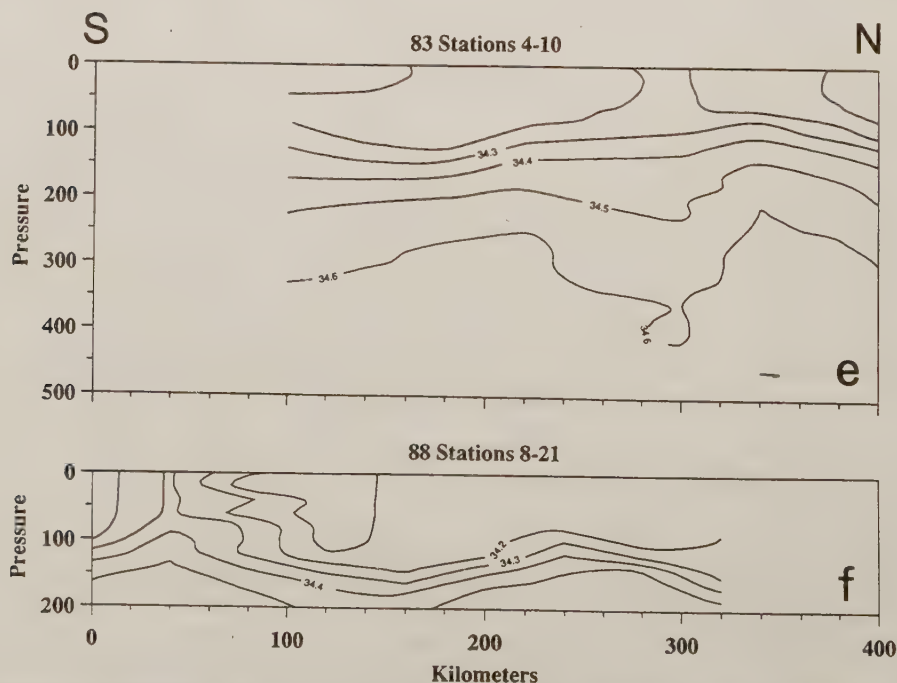


Fig. 9. November 1983 distribution of S along transect e at about 40°W in the southern Scotia Sea (upper) and June 1988 distributions along transect f (lower) which partially overlaps the 1983 transect. Locations are shown on Figs. 1 and 2.

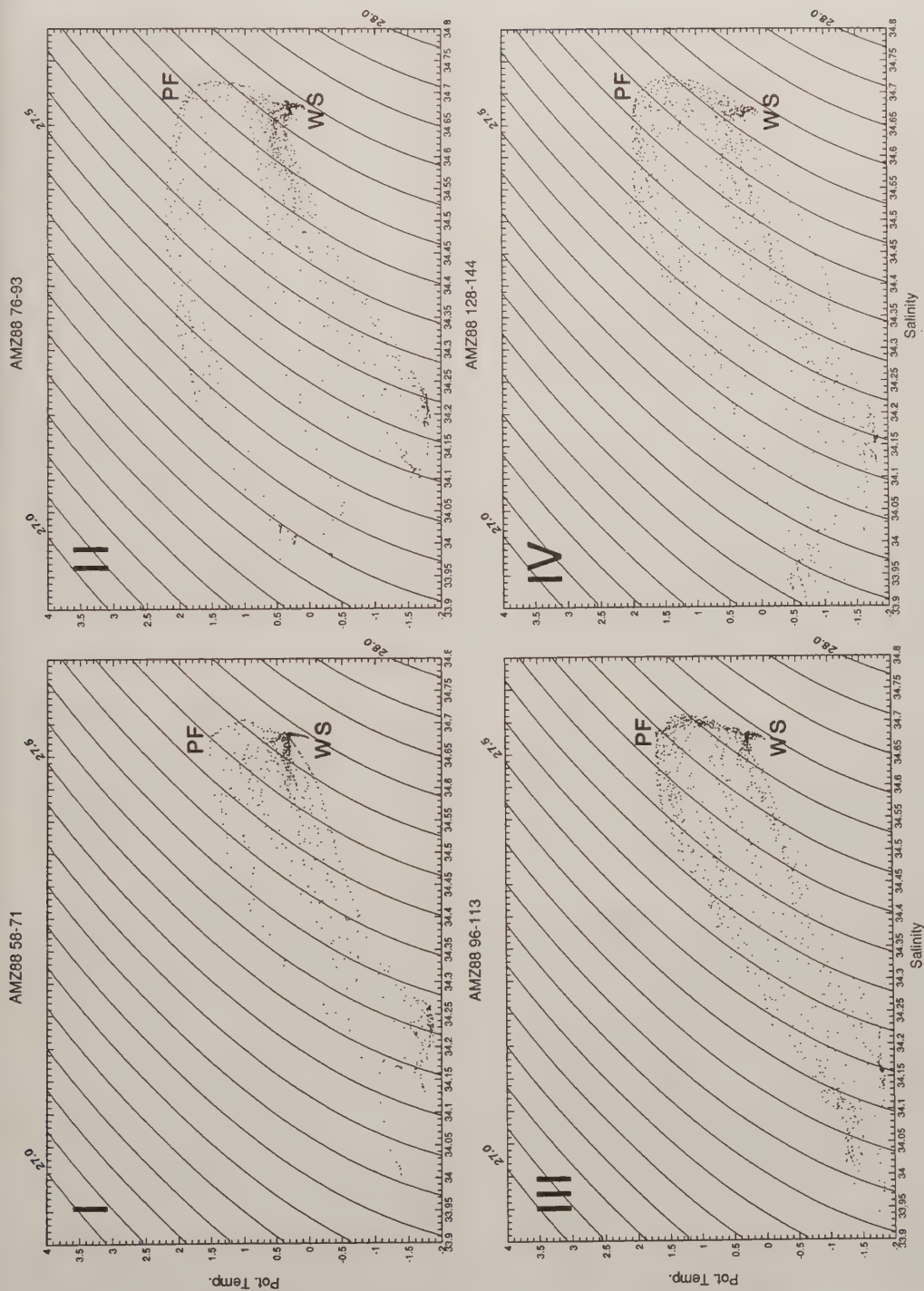


Fig. 10. Potential temperature-salinity diagrams, derived from July-August 1988 CTD data, illustrating the water masses found in the northwestern Weddell Sea and southern Scotia Sea region. One set of end-point characteristics is provided by Polar Front Water (labeled PF), the other is provided by Weddell Sea water (labeled WS). Diagram I shows characteristics along the 35°W transect, II along 40°W, III along 44°W, and IV along 48°. Locations are shown on Figs. 1 and 2.

another mesoscale feature farther east which might have been either an eddy or a meander.

Sea ice conditions in the MIZ

The seasonal sea ice cover is continuous between the Weddell and Scotia seas. The summer ice in the western Weddell is "multi-year" ice (actually, second-year ice as compared to the true multi-year ice which is found in the Arctic Ocean), whereas that found in the Scotia Sea in winter and spring is a mixture of multi-year ice which has been advected northward from the Weddell Sea and young/first-year ice which has been formed locally.

The primary region of ice formation in the Weddell-Scotia Sea system during winter appears to be in areas of divergence in the southern Weddell Sea. Less important and not documented, but perhaps significant, are localized areas of divergence within the pack which manifest themselves as lead fields. The ice drifts northward, during winter, in the western Weddell Sea under the influence of south winds and northward currents. It flows into the Scotia Sea through the gaps overlying the South Orkney Ridge, soon drifting eastward as it enters the strong eastward currents in the southern Scotia Sea. Continually under the influence of south winds and strong east-northeastward currents, the ice soon is advected into warmer water where it melts rapidly, creating upper layer meltwater lenses and localized frontal structures.

The summer Weddell Sea MIZ behaves basically differently, in terms of ice balance, from the winter Scotia Sea MIZ. The Scotia Sea MIZ is the receiving area for a large amount of ice which is continually advected into the region and melts, with the strong regional currents removing meltwater away toward the east-northeast. The Weddell Sea MIZ shows the effects of in situ melting of ice which had been there from the previous winter. However, ice is not generally advected into the Weddell Sea MIZ. Regional ice drift patterns (cf. Ackley, 1979) show that summer drifts tend to be sluggish, compared with winter drift rates, and northward so that there is no mechanism for providing a continual source of ice

into the MIZ. The meltwater lenses found associated with the Weddell Sea MIZ during autumn 1986 were remnants of features from ice melting throughout the preceding summer. Those found along the spring and winter Scotia Sea MIZ were, in contrast, being actively generated and advected away from the region during the observation period.

There is little evidence, with respect to horizontal circulation processes, that the pack ice cover serves as other than a seasonally varying passive tracer whose drift responds to winds and currents. The ice exerts considerably greater control, however, over vertical processes by influencing vertical stratification. Because the Weddell Sea, as compared to the Scotia Sea, is dominated by vertical processes, the ice cover must interact to a greater extent with the Weddell than with the Scotia Sea water column. In the Weddell, the effect is to reduce vertical stability through brine formation, whereas in the Scotia the effect is to increase upper layer stability through melting.

Water masses

Waters enter our study region from the eastern Weddell Sea, from Bransfield Strait and from Drake Passage. The former waters may undergo some modification through vertical processes during their passage through the western Weddell Sea (e.g. Foster and Carmack, 1976; Muench et al., 1990a), however, they appear to fit within a well defined envelope by the time they exit the Weddell Sea via northward flow along the Antarctic Peninsula and for our purposes here may be regarded simply as Weddell Sea Water. This cold, dense water provides an endpoint, in terms of water mass mixing, on a potential temperature-salinity diagram (Fig. 10).

On entering the southern Scotia Sea, Weddell Sea water converges immediately with Scotia Sea water which is warmer, less saline and less dense. The Scotia Sea water includes a variety of water types ranging from relatively warm ($\sim 2^{\circ}\text{C}$ at the subsurface core) Polar Front Water to colder water which may have originated from Bransfield Strait (Fig. 10). Subsurface Weddell Sea water mixes along isopycnal surfaces, which can be seen

both as interleaving both on the vertical sections and on the potential temperature–salinity plots. It is noted, however, that temperature–silicate characteristics typical of the Weddell regime are observed in the southern Scotia Sea as well and are indicated by high silicate values ($\sim 80 \mu\text{mol/l}$ in the upper mixed layer; L. Gordon, Oregon State Univ., 1990 pers. commun.) and a low maximum T .

Previous workers in the region have noted a zonally oriented band, centered roughly on the South Scotia Ridge, of complex mesoscale activity and lowered vertical stability. This anomalous water structure was not derivable through mixing of the source waters described above, and was hypothesized as being due to deep winter convection (Deacon and Moorey, 1975) or to oceanic lateral boundary layer mixing acting on waters in Bransfield Strait and the continental margin regions to the west (Patterson and Sievers, 1980). While the corresponding surface salinities were in some cases as high as previously reported WSC values, salinities observed at the temperature maximum were lower than those indicative of WSC water (Gordon et al., 1977). Apparently, near-surface lateral mixing processes produce WSC surface characteristics, but development of the deeper characteristics of the WSC require more extensive vertical mixing. This may mean either that the feature is seasonal, present only in-summer, or that the 1983 and 1988 sampling patterns were too far east to sample it. The winter 1988 data were adequate, however, to discount significant vertical convection in the southern Scotia Sea (Muench et al., 1990b). Upper layer stability was increased by continuing melting of ice in the MIZ, rather than being lowered as would occur if significant freezing and brine rejection were occurring.

Summary

The following specific points result from our analyses:

- The regional circulation extends continuously from the northwestern Weddell into the southern Scotia Sea. However, the Weddell Sea upper

layer water mixes isopycnally with deeper layers in the Scotia Sea.

- The Scotia Sea is characterized by a very high level of mesoscale activity, reflecting its highly energetic current regime and the convergence there of water masses from the Weddell Sea and from Drake Passage. The northwestern Weddell Sea is characterized, in contrast, by a virtually complete lack of mesoscale activity and by very weak mean currents.

- The ice balance in the MIZ differs between the northwestern Weddell and southern Scotia Sea regions. In the former region, ice melt accumulates through the summer to form upper layer lenses and fronts along the MIZ which are essentially remnant features. In the latter region these lenses and fronts are actively formed as ice is advected into the MIZ and melts.

- Wintertime upper layer stratification in the southern Scotia Sea is strengthened by continual advection of sea ice from the south which then melts in the MIZ. In at least partial consequence of this, the southern Scotia Sea is not a site of deep winter convection.

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Great Frigatebird (*Fregata minor*) Predation: Not a Factor in Hatchling Green Turtle (*Chelonia mydas*) Survival at French Frigate Shoals, Hawaii

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Abstract.—Frigatebirds are known predators of sea turtle hatchlings at several locations worldwide. At certain localities this predation might exacerbate the already endangered status of these marine reptiles. French Frigate Shoals, Hawaii is where over 90% of all Hawaiian green turtle (*Chelonia mydas*) breeding occurs and is the site of a large Great Frigatebird (*Fregata minor*) colony. Frigatebird predation was not a factor in hatchling survival at this location. We found no evidence of green turtle hatchlings in the stomach contents of 200 Great Frigatebirds sampled during peak periods of hatchling emergence in 1988 and 1989. Received 3 June 1991, accepted 21 November 1991.

Key words.—*Chelonia mydas*, *Fregata minor*, Great Frigatebird, green turtle, Hawaiian Islands, predation.
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In 1978, the Hawaiian green turtle (*Chelonia mydas*), with all other sea turtles under United States jurisdiction, was protected under provisions of the U.S. Endangered Species Act and a recovery plan for Hawaiian sea turtles (Balazs *et al.* 1990) was subsequently prepared. Because frigatebirds (*Fregata* spp.) prey on hatchlings in certain other *Chelonia* populations (Hirth 1971, Stancyk 1982), one of the actions recommended in the recovery plan was to investigate the extent of seabird predation on turtle hatchlings. We studied Great Frigatebird (*Fregata minor*) predation on green turtle hatchlings at French Frigate Shoals, Hawaii, where over 90% of all Hawaiian green turtle breeding occurs (Balazs 1980). Adult turtles from throughout the Hawaiian Archipelago migrate to this area to nest (Balazs 1976).

STUDY AREA AND METHODS

French Frigate Shoals is a crescent-shaped atoll, 16 km in diameter, situated near the midpoint of the Hawaiian Archipelago. The atoll, part of the Hawaiian Islands National Wildlife Refuge, consists of 11 sandy islets and one volcanic pinnacle (for detail, see Amerson 1971).

In 1988 and 1989, we sampled stomach contents of Great Frigatebirds during the peak period of turtle hatchling emergence at French Frigate Shoals. To determine peak hatchling emergence, we monitored green turtle nesting activity on Tern Island by con-

ducting daily surveys of the island. We marked all turtle nests on the island and estimated their hatch dates based on a mean incubation period of 64.5 days (Balazs 1980). To verify the accuracy of the estimated period of peak hatchling emergence, nests were monitored until hatchlings emerged. Periodically, we visited the other islands to confirm that Tern Island data were representative of nesting activity throughout the atoll.

During the peak period of turtle hatchling emergence, we counted the number of Great Frigatebirds on Tern Island. Counts were conducted on windless evenings, when most frigatebirds at French Frigate Shoals roosted on Tern Island, and included adults, juveniles, and nestlings. Adults and juveniles were distinguished by their plumage characteristics. The juvenile category included subadults, immatures, and juveniles, as classified by Harrison (1983). The nestling category included flightless chicks and fledged chicks that were still being fed by their parents.

We captured frigatebirds by hand or with long-handled fish nets. We obtained stomach contents by inducing regurgitation by pumping seawater into the birds' stomachs (Wilson 1984). Stomach contents were emptied into a fine-mesh strainer and examined for evidence of turtle hatchlings. We identified contents to the family level when possible using Tinker (1982). The "unidentified fishes" prey category consists of partially digested fishes that could not be identified.

Because few frigatebird stomachs contained prey in the early morning hours, in 1988 we collected one-third of the samples in each of the following time periods: 1200-1400 h, 1730-1830 h, and 2000-2115 h. In 1989, we collected half of the samples between 1000 and 1200 h and the remainder between 1845 and 1930 h. All stomach content calculations are based upon only those birds which contained food items.

RESULTS

Turtle nesting occurs on six of the sandy islets with about 90% of the nesting activity occurring on East and Whaleskate islands (Balazs 1980). Most of French Frigate Shoals' Great Frigatebird population nests on Tern Island, where there is a nesting colony of about 700 pairs. Few frigatebirds nest or roost on the other islets. However, frigatebirds from Tern Island feed throughout the atoll and in surrounding waters.

We estimated that 412 and 552 female green turtles nested at French Frigate Shoals during 1988 and 1989, respectively. Based on average clutch size, number of clutches laid per female, hatching success, and emergence success, we estimated that 106,000 hatchlings were available to frigatebirds in 1988 and 163,000 in 1989.

Comparison of data from our Tern Island turtle nest monitoring with observations of nesting activity on the other islets showed that hatchling emergence phenologies on all the islets were similar; turtle hatchlings emerged between early July and late December. Hatchling emergence peaked in September in both years.

During peak turtle hatchling emergence, numbers of Great Frigatebirds at French Frigate Shoals varied greatly between the two years. In 1988, about 15,000 frigatebirds, mostly adult females and immatures, roosted on Tern Island. The following year only about 4,000 frigatebirds were present. In both years, juvenile birds accounted for about half of the frigatebird population.

Between 12 and 28 September 1988, we analyzed stomach contents of 150 Great Frigatebirds (50 each of adults, juveniles, and nestlings). Stomach contents of another 50 nestlings were analyzed between 16 and 18 September 1989. No turtle hatchlings were found in any of the frigatebird stomachs sampled. We found prey items in 110 (73.3%) of the 150 birds sampled in 1988 (Table 1) and in 34 (68.0%) of the 50 frigatebird nestlings sampled in 1989. In 1988, the Fan-tail Filefish (*Pervagor spilosoma*) was the most important prey. No filefish were found in the 1989 samples, when flying fish and squids each contributed 38.2% of the 144 food items iden-

tified. The remaining 23.6% items were unidentified fishes.

DISCUSSION

Turtle hatchlings emerge predominately at night (Balazs 1980). After entering the water, they rapidly swim out to sea. Although little is known about the behavior of hatchlings at sea, they are probably restricted to the surface zone where they feed on macroplankton (Hirth 1971).

Because of their inability to take off from water, Great Frigatebirds feed by snatching prey from surface waters (Harrison *et al.* 1983) and by pirating food from other seabirds; however, pirating has been shown to be less significant than once thought (Nelson 1975, Schreiber and Hensley 1976). Most frigatebird feeding activity takes place in the daylight hours (Schreiber and Clapp 1987), and Nelson (1975) reported that Great Frigatebirds are reluctant to take food from land (except chicks of other seabirds). These factors limit the opportunity for frigatebirds to take turtle hatchlings during their nocturnal postemergence dash to the sea. We have not observed Great Frigatebirds attempting to take turtle hatchlings from land, not even when misdirected hatchlings are still wandering around the interior of the island after sunrise.

Although nestling frigatebirds do not capture prey themselves, we sampled the contents of their stomachs. Adults, needing to supply food to ravenous nestlings, may be more opportunistic in their prey selection, taking a wider variety of prey items. Therefore, stomach contents of nestlings needed to be examined. If parental food requirements do not alter prey selection, prey items fed to the nestlings should be representative of the adults' diet.

Turtle hatchlings should be available to frigatebirds in the waters surrounding the atoll. However, we found no evidence of turtle hatchlings in the stomach contents of the 200 Great Frigatebirds that we sampled. Harrison *et al.* (1983) found no green turtle hatchlings in 284 Great Frigatebird regurgitations collected throughout the northwestern Hawaiian Islands during all months except December and January.

Table 1. Stomach contents of adult, juvenile, and nestling Great Frigatebirds collected at Tern Island, French Frigate Shoals, during September 1988.

Prey	Adults (40 birds)		Juveniles (36 birds)		Nestlings (34 birds)		Combined (110 birds)	
	N(%) ¹	% Occur. ²	N(%)	% Occur.	N(%)	% Occur.	N(%)	% Occur.
Fishes	220(97.8)	100.0	135(97.8)	97.2	186(76.9)	88.2	541(89.4)	95.5
Filefish (Monacanthidae)	194(86.2)	77.5	108(78.3)	75.0	110(45.5)	44.1	412(68.1)	66.4
Flying Fish (Exocoetidae)	6(2.7)	5.0	20(14.5)	16.7	56(23.1)	35.3	82(13.6)	18.2
Tuna (Scombridae)	3(1.3)	2.5	1(0.7)	2.8	—	—	4(0.7)	1.8
Unidentified	17(7.6)	20.0	6(4.3)	8.3	20(8.3)	26.5	43(7.1)	18.2
Squid	5(2.2)	5.0	3(2.2)	5.6	56(23.1)	38.2	64(10.6)	15.5

¹N = number of food items in the category (% of the total number of food items).²% Occurrence = the percentage of birds that contained that prey type.

Balazs (1980) found no evidence of turtle hatchlings in fecal matter at Great Frigatebird nesting and roosting sites at French Frigate Shoals. Therefore, we conclude that Great Frigatebird predation in the vicinity of French Frigate Shoals is not a factor in green turtle hatchling survival.

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Sulfide detoxification and tolerance in *Halicryptus spinulosus* (Priapulida): a multiple strategy

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ABSTRACT: The detoxification potential of *Halicryptus spinulosus* in the presence of sulfide was studied. The worms are able to cope with considerable amounts of sulfide. They benefit from several survival strategies for controlling sulfide dose and detoxifying sulfide that enters the body. When oxygen and sulfide occur concurrently in the environment sulfide can either initially be excluded or internal concentration kept low by the animals. Non-toxic thiosulfate, the main detoxification product, accumulates up to $3856 \pm 997 \mu\text{M}$ in the hemolymph. Sulfide has an overriding influence on the aerobic metabolism and imposes anaerobiosis even though oxygen is available, i.e. sulfide-induced anaerobiosis. Succinate, an indicator of anaerobic metabolism, accumulates during persistent oxic sulfide incubation to $12.3 \pm 2.3 \mu\text{mol ml}^{-1}$ in hemolymph and to $3.0 \pm 1.3 \mu\text{mol g}^{-1}$ fresh mass in body wall after 10 d. During anoxic sulfide exposure, the animals make use of graded strategies. Some sulfide is immobilised in an external barrier due to iron-sulfide formation. The iron-sulfide compound results in a conspicuous blackening of the animal and its blood. This blackening is fully reversible upon receiving oxygen again. Detoxification to thiosulfate, depending on the oxygen storage capacity of the hemolymph, amounted to only a minor level, with a maximum of $172 \pm 49 \mu\text{M}$ in the hemolymph after 1 d of incubation. Sulfide also binds to a presently unknown hemolymphic factor. This binding may temporarily protect mitochondria, a main location of sulfide detoxification. The mitochondrial enzyme for aerobic metabolism, cytochrome c oxidase, is inhibited by low sulfide levels *in vitro* (K_i $1.05 \pm 0.22 \mu\text{M}$), and has a much higher *in vivo* resistance in whole animals. Catalase, another sulfide sensitive enzyme, has a K_i of ca $200 \mu\text{M}$ *in vitro* and is unaffected *in vivo*. Internal sulfide concentration in the hemolymph increases ca 3-fold ($570 \pm 298 \mu\text{M}$) over external levels during long-term exposure experiments with $200 \mu\text{M}$ sulfide. The survival in spite of such an elevated amount of internal sulfide accumulation is unprecedented for a marine invertebrate without endosymbionts. The worms can passively outlast raised environmental sulfide concentrations by their high capacity for anaerobic metabolism.

INTRODUCTION

Recent studies stress the importance of sulfide in a variety of marine environments other than deep-sea hydrothermal vents (Bagarinao & Vetter 1989, 1990, Cary et al. 1989b, Schiemer et al. 1990, Llansó 1991, Ott et al. 1991, Vismann 1991a, Völkel & Grieshaber 1992).

Although sulfide has been known to be abundant in marine sediments, this highly toxic compound has usually been disregarded as a factor influencing the distribution of soft bottom benthic macrofauna. Exposure and impact of sulfide on marine invertebrates have

attained considerable attention during the last years due to the discovery of the spectacular deep-sea hydrothermal vents (for reviews e.g. Somero et al. 1989, Fisher 1990), which has stimulated intensive research on this topic. The well-aerated sulfide-containing deep-sea vents are mostly inhabited by flourishing populations of marine macrofauna with sulfide-oxidising endosymbiotic bacteria (e.g. Cavanaugh et al. 1981, Powell & Somero 1983, Jones 1985, Fisher 1990).

Sulfide-rich marine soft sediments have different features. Constant anoxic sulfidic sediments like those of the deep basins of the Black Sea and the Baltic Sea are without higher organisms and only the borders of these areas are colonised by some invertebrates. A different situation is encountered in areas with sea-

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sonal fluctuations of oxygen availability and subsequent sulfide development. Sulfide is produced in the anoxic sediment layers. When oxygen becomes limited the anoxic layer with the sulfide expands upwards. Such biotopes are either populated by opportunistic species with little or no capacity for anaerobic metabolism or by species with an extraordinary anaerobic capacity and sulfide resistance. Opportunistic species are able to survive only during intermittent periods when oxygen is available and sulfide is absent. With deteriorating conditions these populations will be extinguished. In areas like those of the Western Baltic only a few species are able to resist frequent adverse environmental conditions. Earlier studies on such species showed a high anaerobic capacity (Theede et al. 1969, Theede 1984, Oeschger 1990). The importance of anaerobiosis as a strategy to avoid sulfide toxicity has yet to be intensively addressed.

Halicryptus spinulosus, a priapulid worm and one of those few species able to persist in anoxic soft sediments of the Western Baltic, is frequently exposed to elevated sulfide levels. It is an important faunal component with high abundances and it survives for extended periods at environmental anoxia (Weigelt & Rumohr 1986). Previous studies on *H. spinulosus* dealt with its anaerobic capacity (Oeschger 1990, Oeschger & Storey 1990), energetic studies (Oeschger et al. 1992), and with histological and ultrastructural peculiarities of sulfide impact on the animals (Oeschger & Janssen 1991, Janssen & Oeschger 1992).

The objective of this paper was to study sulfide detoxification and tolerance in *Halicryptus spinulosus*. We conducted studies on whole animals to look at the oxic and anoxic sulfide detoxification potential and to assess the involvement of an anaerobic metabolism. Further points of interest were the effects of sulfide exposure on enzymes. Shipboard studies on the actual sulfide contents in worms and the sediment were performed to complete this study.

MATERIAL AND METHODS

Sampling. *Halicryptus spinulosus* were dredged during several cruises between summer 1990 and winter 1991/92 from muddy soft sediments at a water depth of 20 m in Kiel Bight, Western Baltic Sea. Specimens were transported live in a cooler to the Scripps Oceanographic Institution, La Jolla, California, USA, in summer 1990. They were kept unfed in aerated seawater at $9.5 \pm 0.5^\circ\text{C}$ and 22‰ S in original sediment. Prior to experiments worms were kept at least 5 d in aerated seawater without sediment.

During 1990 to 1992 some worms were analysed for sulfide contents directly after capture aboard the

research vessel. In November 1991 a specially designed light-weight gravity sediment corer (Meischner & Rumohr 1974) was used from shipboard to obtain pore water from undisturbed sediment cores (diameter 80 mm) of the sampling area. Sediment was centrifuged immediately aboard ship and analysed for sulfide contents after Cline (1969), using the 1 to 40 μM range of reagents.

Oxic sulfide incubation. A continuous flow-through system with a chamber volume of about 1.5 l was used. A peristaltic pump delivered supersaturated (107%) seawater ($10 \pm 0.5^\circ\text{C}$, 22‰ S) at a constant flow rate of about 800 ml h^{-1} . A sulfide stock solution (3.2 mM, pH adjusted with HCl to 7.0) was delivered by another peristaltic pump and mixed with seawater before entering the incubation chamber to obtain the experimental concentration. During the experiments oxygen and sulfide concentrations were regularly monitored. For oxygen measurements a modified Winkler procedure (after Ingvorsen & Jørgensen 1979) had to be used due to sulfide interaction with the conventional determination: sulfide was precipitated with 2 N ZnSO_4 in the presence of 1 N NaOH and oxygen could then be reliably estimated in the overlying seawater. Oxygen concentrations were mainly in the range of 90 to 97%, referred to as 'oxic incubation'. Sulfide concentrations were in the range of $200 \pm 40 \mu\text{M}$ and pH in the chamber was between 7.84 and 7.98. In this paper the term sulfide refers to total sulfide (H_2S , HS^- and S^{2-}) unless otherwise stated.

Anoxic sulfide incubation. For anoxic sulfide exposure experiments (200 μM), worms were incubated in an airtight experimental chamber containing 500 ml seawater ($9.5 \pm 0.5^\circ\text{C}$, 22‰ S). Sulfide levels were obtained by adding $\text{Na}_2\text{S} \cdot 9\text{H}_2\text{O}$ crystals to nitrogen or argon-bubbled oxygen-free seawater to a given final concentration of ca 200 μM and pH was adjusted to 8.0 with HCl. After sealing the chamber, an argon atmosphere was introduced to cover the surface additionally against oxygen. During exposure experiments triplicate water samples were taken and the sulfide concentration was measured by the methylene blue method (Cline 1969). Due to oxidation during incubation, H_2S concentrations were readjusted daily to the intended level. This happened particularly during the first 3 to 4 d of incubation, while sulfide concentration was nearly unchanged afterwards. To avoid the accumulation of toxic metabolites, the seawater was changed every 3 to 4 d. For anoxic sulfide exposure we chose a concentration of 200 μM since this is a realistic concentration that the worms encounter during long-term environmental oxygen deficiency.

Enzyme assays. **Cytochrome c oxidase:** Activity of cytochrome c oxidase (E.C. 1.9.3.1) in freshly sampled body wall tissue and hemolymph of *Halicryptus*

spinulosus was measured after Hand & Somero (1983). *In vitro* sulfide inhibition experiments were performed on homogenates from unexposed worms using different sulfide concentrations to calculate the 50 % inhibition constants (K_i or I_{50} -value). Activity of cytochrome c oxidase was also assayed in specimens exposed to 200 μ M sulfide for 8 d (22‰ S, $9.5 \pm 0.5^\circ\text{C}$).

Catalase: Activity of catalase (E.C. 1.11.1.6) was determined according to Aebi (1985). Samples were homogenised in 40 mM potassium phosphate buffer. The homogenate was assayed in potassium phosphate buffer (50 mM, pH 7.0) containing H_2O_2 as substrate (35 μ l of a 30 % H_2O_2 stock solution diluted with 10 ml of phosphate buffer). From this solution, 350 μ l were added with a varying volume of phosphate buffer and homogenate to a final volume of 1 ml. The initial absorbance at 240 nm was in the range of 0.500, and time needed for a decrease from 0.450 to 0.400 was recorded to calculate the activity of catalase. Since this reaction exhibits abnormal kinetics, the rate constant of the first order reaction [k , according to the equation $k = 1/t \cdot \ln(E_0/E)$] has to be converted to units. One unit is defined as the decomposition of 1 μ mol $\text{H}_2\text{O}_2 \text{ min}^{-1}$, while the concentration of H_2O_2 decreases from 10.3 μ mol ml^{-1} ($\text{abs}_{240} = 0.450$) to 9.2 μ mol ml^{-1} ($\text{abs}_{240} = 0.400$).

Bovine liver catalase (Sigma) was used as a reference standard. Sodium azide (1 mM) was used as an inhibitor of catalase. *In vitro* inhibition of different concentrations of sulfide were assayed and I_{50} -values were calculated.

Succinate. The anaerobic metabolite succinate was measured using the standard enzymatic determination after Beutler (1985).

Chromatography of sulfur compounds in body wall tissue and hemolymph. Determination and quantification of sulfur compounds was done by reversed-phase high-performance liquid chromatography (HPLC) (Fahey & Newton 1987, Vetter et al. 1989), with monobromobimane (mBBR), a synthetic molecule that covalently binds reduced sulfur compounds (thiols) and makes them fluorescent. The term 'thiol' refers to sulfhydryl compounds which react with mBBR. In this paper the term is extended to sulfite, sulfide and thiosulfate. Samples were run on a computer-controlled Kontron HPLC system, excitation wavelength of the detector was set at 350 nm, emission wavelength on 480 nm. Quantification was achieved by comparing the peaks with authentic standards: fluorescence of the sulfur compounds in the samples was measured against standard mixtures of sulfide, thiosulfate, sulfite, cysteine, and glutathione. To ascertain that the peaks detected were sulfur compounds, a subsample was derivatized with non-fluorescent 2-dipyridyl-sulfide (PDS), which also binds sulfur species but prevents

mBBR binding. After the experiments, body wall tissue was immediately homogenised in an ice-cold HEPES-buffer (N-2-hydroxyethylpiperazine-N'-2-ethane sulfonic acid, 200 mM, pH 8.0) containing the mBBR and prepared for further HPLC analysis (Vetter et al. 1989). Hemolymph was prepared without pretreatment. Samples were either directly analysed or stored at 4°C . Storage at 4°C had no significant effect on content of sulfur compounds (Fahey & Newton 1987).

In some experiments oxidation of sulfide and conversion to other metabolites was studied using radiolabelled Na_2^{35}S (Amersham). The HPLC system was able to detect fluorescence and radioactivity of ^{35}S simultaneously, the latter by a flow-through in-line scintillation counter (Vetter et al. 1989).

Hemolymph binding. To detect the possible presence of a sulfide binding component in the hemolymph of *Halicryptus spinulosus*, we used ^{35}S -radiolabelled sulfide in connection with a dialysis chamber. Hemolymph samples from 4 to 8 unexposed oxic controls, or anoxic worms which had been exposed for 10 d to a sulfide concentration of 200 μ M, were placed in plugged cylinders of dialysis tubing (molecular weight cut off: ca 12 kDa) using a Hamilton syringe (final sample volume: 1 ml). The dialysis bag was placed in a water-jacketed stirring reservoir of 12 ml buffer volume (seawater of 22‰ S, buffered with 10 mM Tris, pH 7.5). Control samples without hemolymph consisted of buffered seawater and were also placed in separate dialysis bags. Cold and radiolabelled sulfide was added to the outer buffer to a final concentration of 200 μ M in a ratio 3:1. The buffer was moderately degassed prior to use to prevent an immediate spontaneous oxidation of the sulfide. Repeated sampling and scintillation counting of the ^{35}S radioactivity in the samples and the control bag showed the diffusion and final equilibrium. The measure for binding capacity was the difference in counts between buffer control and hemolymph samples.

Isolation and respiration of mitochondria. For one mitochondrial isolation, ca 15 to 20 worms (8 to 9 g fresh mass) were homogenised. The body wall of freshly dissected worms was cleansed of adhering coelomic fluid and other tissues, rinsed in isolation buffer, and cut in coarse pieces. This suspension was homogenised using a 10 to 15 s burst (9500 rpm) of an Ultra Turrax tissue homogenizer, and further homogenised in a Potter-Elvehjem homogenizer with 3 to 5 passes of a teflon pestle (final volume: ca 8 to 9 g fresh mass per 30 ml isolation buffer). The isolation buffers consisted of 350 to 500 mM glycine, 170 to 200 mM sucrose, 2 mM EGTA [ethylene glycol-bis-(β -aminoethyl ether) N,N,N',N'-tetraacetic acid], 2 mM EDTA (ethylene diamine-N,N,N',N'-tetraacetic acid), 25 to 100 mM KCl, 20 mM HEPES, 0.2 % BSA (bovine

serum albumin, essentially fatty acid free), pH 7.4. The resulting preparation was centrifuged at 600 *g* for 6 min to remove cellular debris. A second spin at 13 500 *g* for 15 min was used to pellet the mitochondria of the supernatant of the first spin. The upper layer of the resulting pellet was resuspended in 0.5 to 1 ml of isolation buffer. Any further purification steps lead to significantly reduced or no mitochondrial activity and were omitted. Activity of GDH (glutamate dehydrogenase) was used as a mitochondrial marker enzyme. Mitochondrial preparations usually contained 2 to 4 mg protein ml⁻¹ (determined by the Biuret method).

Assays of mitochondrial respiration were monitored at 13°C in an oxygen respiration chamber described by O'Brien & Vetter (1990) to determine the respiratory control ratio (RCR) (Estabrook 1967). The respiration medium was the same as used for isolation plus up to 10 mM potassium phosphate and 7 mM 2-oxoglutarate. For oxygen respiration measurements of the mitochondria, a gold-coated sulfide-insensitive Clark type oxygen electrode (Eschweiler, Kiel, Germany) was used.

RESULTS

Environmental sulfide

Sediment

In Fig. 1 the sulfide concentration in the pore water of the sampling location in November 1991 is shown (Western Baltic Sea: 54° 38.1' N, 10° 20.5' E; water depth 21 m). *Halicryptus spinulosus* is found down to 30 cm sediment depth. Results indicate that the worms can be exposed to a concentration of up to 665 µM sulfide in the pore water. On earlier cruises the directly measured sulfide concentrations in samples of pooled pore water from 0 to 5 cm sediment depth were: 30 to 49 µM (27 November 1990); 4 to 29 µM (27 February 1991), and 2 to 16 µM (2 July 1991).

Worms

In Table 1 sulfide and thiosulfate concentrations in worms from different cruises are compiled. Hemolymph samples were taken on shipboard immediately after obtaining the worms to determine actual *in situ* values. Some *Halicryptus spinulosus* were subsequently kept in the laboratory in aerated seawater without sediment to monitor the course of the sulfide and thiosulfate concentration. On some occasions nearly all dredged *H. spinulosus* were black, reflecting sulfide exposure. During collection, both pale to brownish-looking and black worms were caught, indi-

cating a patchy distribution of sulfide in their habitat. Internal sulfide concentrations decreased during the laboratory incubation and thiosulfate was not detectable, with one exception showing small amounts.

Sulfide incubation experiments

Whole animals

Halicryptus spinulosus usually has a pale to dark brown colour when living in oxidised sediment without sulfide. During the experiments some individuals started to turn black on the surface of their body wall after only about 1 h exposure to 200 µM sulfide containing anoxic seawater. The blackening intensified after 2 h and the body wall of all worms was completely black after 5 to 6 h of incubation, whereas the hemerythrin-containing hemolymph turned completely black after ca 3 d of incubation.

On one occasion we observed that the process of regaining the usual pale brown colour after being transferred to aerated seawater started from the middle of the body wall, and the worms regained their normal colour within 1 to 2 min. Such a rapid colour change might indicate the involvement of an enzyme-mediated mechanism in reversing the iron-sulfide interaction. During oxic sulfide incubation (200 µM) about 50 % of the worms turned black after ca 3 d, but not as intensely as during anoxic sulfide incubation.

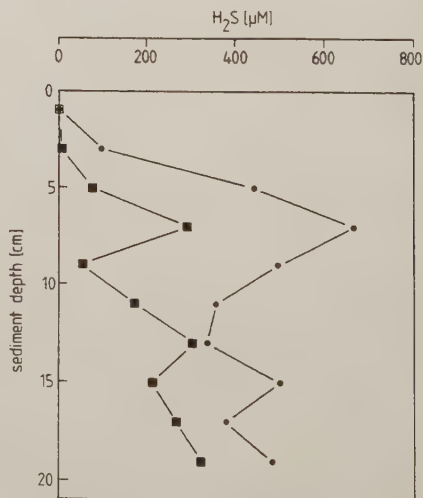


Fig. 1. Sulfide concentration in pore water (in µM) from the sampling location of *Halicryptus spinulosus* in the Western Baltic Sea in November 1991 determined by the methylene blue method. (●) Core 1; (■) Core 2

Sulfide concentration in whole animals was $6.6 \pm 4.3 \text{ nmol g}^{-1}$ fresh mass ($n=5$), while thiosulfate levels were $1.02 \pm 1.39 \text{ nmol g}^{-1}$ fresh mass ($n=5$).

Body wall

During oxic sulfide incubation (200 μM), sulfide started to accumulate in body wall tissue of *Halicryptus spinulosus* from an initial $0.028 \pm 0.014 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=4$) in control worms to $0.106 \pm 0.164 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=4$) after 1 d of exposure. After 10 d, sulfide concentration rose to $0.201 \pm 0.072 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=6$) (Fig. 2a). Thiosulfate, an oxidation product of sulfide, increases strongly after 1 d of incubation from an initial $0.07 \pm 0.03 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=4$) to $0.275 \pm 0.143 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=5$), reaching a maximum of $0.779 \pm 0.14 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=5$) after 4 d. Thiosulfate concentration tended to decrease to $0.422 \pm 0.17 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=5$) at the end of the experiments (Fig. 2b).

In anoxic sulfide incubations (200 μM), a large accumulation of sulfide was measured in worms. Values increased from $0.079 \pm 0.037 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=6$) in controls to $0.644 \pm 0.286 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=14$) after 10 d. We assessed a possible effect of the mucus covering the outer body wall on sulfide values in body wall tissue. Some samples of a 10 d anoxic incubation (200 μM) were sonicated for 30 s to strip off the mucus prior to analysis. Values of $0.487 \pm 0.398 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=8$) for sonicated tissues tended to be

smaller compared to untreated individuals. After sonication worms were almost pale; their creamy looking gonads and the black hemolymph became visible.

Only minor amounts of thiosulfate were produced after 1 d of incubation ($0.036 \pm 0.027 \text{ } \mu\text{mol g}^{-1}$ fresh mass, $n=5$) and tended to accumulate at the end of the 10 d experiments ($0.092 \pm 0.045 \text{ } \mu\text{mol g}^{-1}$ fresh mass, $n=14$). During anoxic sulfide incubations, thiosulfate concentrations amounted to only a minor fraction of that found during oxic sulfide incubation. Sulfite (SO_3^{2-}), GSH (reduced glutathione) and cysteine were also measured. Sulfite and cysteine were detectable only in traces in control individuals as well as in incubated specimens (data not shown). The concentration of GSH did not differ significantly during the course of the experiments. Concentrations ranged from $0.462 \pm 0.17 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=7$) in controls to $0.40 \pm 0.118 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=6$) in oxic incubated specimens after 10 d, and to $0.448 \pm 0.114 \text{ } \mu\text{mol g}^{-1}$ fresh mass ($n=14$) after 10 d of anoxia.

Hemolymph

In a short-term experiment 100 μl of hemolymph was incubated with ^{35}S -sulfide for 6 h. Analysis showed some ^{35}S -sulfate formation due to chemical oxidation, suggesting that sulfate did not participate in sulfide detoxification. Double radiolabelled thiosulfate (^{35}S - $^{35}\text{SO}_3^{2-}$) was identified as the detoxification product.

At the beginning of oxic sulfide incubation (200 μM),

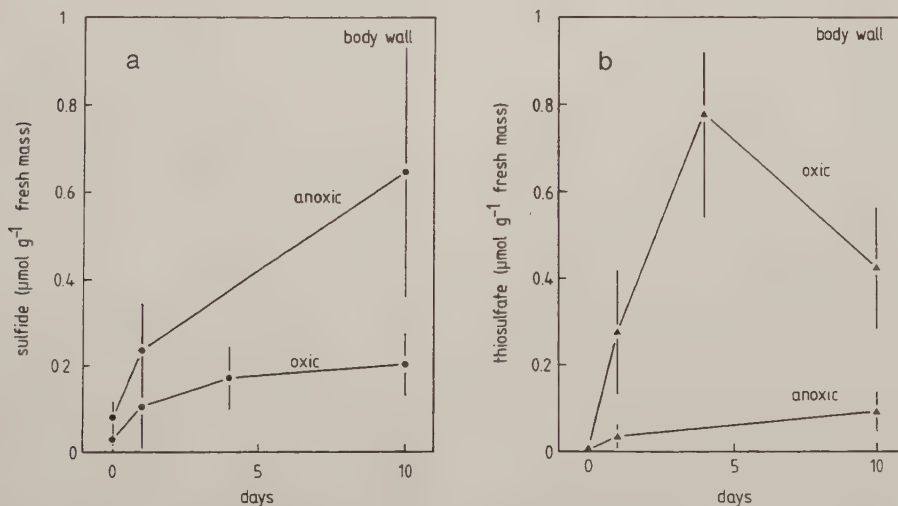


Fig. 2. *Halicryptus spinulosus*. Concentrations ($\pm$ SD) of (a) sulfide and (b) thiosulfate in body wall tissue during oxic and anoxic sulfide incubation after 1, 4 and 10 d at an external sulfide concentration of 200 μM in seawater ($9.5 \pm 0.5^\circ\text{C}$, 22‰ S). Values are in $\mu\text{mol g}^{-1}$ fresh mass. Data are means of 5 to 14 individuals

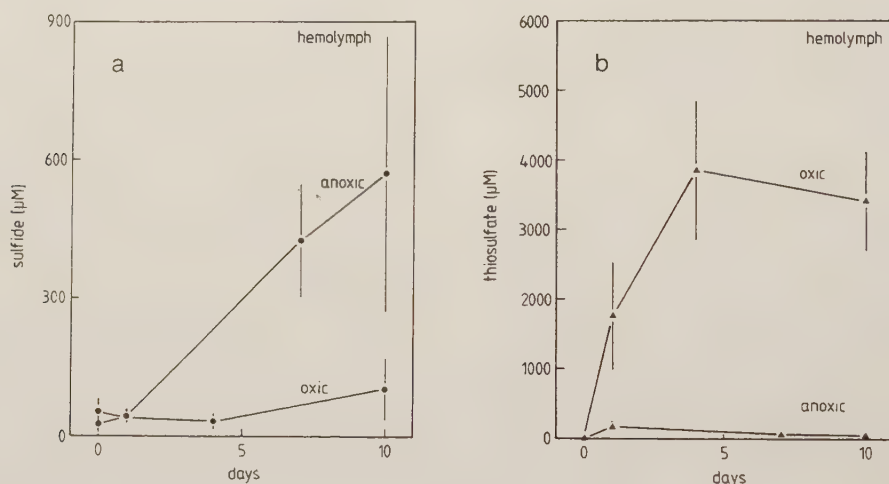


Fig. 3. *Halicryptus spinulosus*. Concentrations ($\pm$ SD) of (a) sulfide and (b) thiosulfate in hemolymph during oxic and anoxic sulfide incubation after 1, 4, 7, and 10 d of an external sulfide concentration of 200 μ M in seawater ($9.5 \pm 0.5^\circ\text{C}$, 22‰ S). Values are in μ M. Data are means of 5 to 18 individuals

Halicryptus spinulosus was able to keep the sulfide from entering the hemolymph. In the course of the experiments, sulfide concentration varied between $53 \pm 29 \mu\text{M}$ ($n = 5$) in controls to $34 \pm 17 \mu\text{M}$ ($n = 5$) after 4 d of incubation, but was $104 \pm 67 \mu\text{M}$ after 10 d ($n = 6$) (Fig. 3a). Thiosulfate increased from $6 \pm 13 \mu\text{M}$ ($n = 5$) in controls to $1756 \pm 781 \mu\text{M}$ ($n = 5$) after 1 d of incubation, reaching a maximum of $3856 \pm 997 \mu\text{M}$ ($n = 5$) at 4 d, while it tended to decrease slightly to $3410 \pm 718 \mu\text{M}$ ($n = 6$) after 10 d (Fig. 3b).

The hemolymph exhibited a different characteristic during anoxic sulfide exposure (200 μM). After 1 d of incubation sulfide concentration ($43 \pm 15 \mu\text{M}$, $n = 5$) did not differ from controls ($26 \pm 18 \mu\text{M}$, $n = 14$). After 7 d the sulfide level had increased to $424 \pm 122 \mu\text{M}$ ($n = 6$), and reached $570 \pm 298 \mu\text{M}$ ($n = 18$) at the end of the experiments. Thiosulfate concentration accumulated from $0.4 \pm 0.7 \mu\text{M}$ ($n = 13$) in controls to a peak of $172 \pm 49 \mu\text{M}$ ($n = 3$) after 1 d of anoxic incubation and was $56 \pm 29 \mu\text{M}$ after 10 d ($n = 16$).

Sulfite and cysteine were only present in traces and were not involved in sulfide detoxification (data not shown). GSH concentrations showed no variation. The level in hemolymph was $247 \pm 184 \mu\text{M}$ ($n = 11$) in controls and $257 \pm 135 \mu\text{M}$ ($n = 18$) after 10 d of anoxic incubation. In oxic sulfide experiments GSH concentrations were $232 \pm 74 \mu\text{M}$ ($n = 6$) after 10 d.

Sulfide binding in the hemolymph

Freshly sampled hemolymph of *Halicryptus spinulosus* was tested for the presence of a sulfide binding factor by means of equilibrium dialysis against ^{35}S -

radiolabelled sulfide. The hemolymph has a binding factor which concentrates sulfide nearly 2-fold over the external sulfide concentration (Fig. 4). Hemolymph from specimens previously exposed to sulfide (200 μM), and specimens kept in sulfide-free seawater prior to the experiment, bound radiolabelled sulfide, suggesting that some unlabelled sulfide in the hemolymph of exposed worms is exchanged for radiolabelled sulfide during dialysis.

The formation of a black fraction of the hemolymph during sulfide incubation occurs in the erythrocytes, since spinning of sulfide-incubated hemolymph resulted in a black pellet and clear supernatant. Spinning of either untreated hemolymph or lysed erythrocytes by ultrasonification with Centricon molecular weight cut-off membranes (10 kDa) indicated that the black component was associated with the fraction above 10 kDa, since the black fraction did not pass the membrane.

Succinate

During oxic sulfide incubation (200 μM) *Halicryptus spinulosus* accumulated only small amounts of succinate in the beginning of the experiments (Fig. 5). After 4 d, levels of succinate increased significantly in hemolymph ($11.3 \pm 5.1 \mu\text{mol ml}^{-1}$) and body wall ($2.3 \pm 0.9 \mu\text{mol g}^{-1}$ fresh mass) with a trend of further accumulation after 10 d of incubation. This indicated that the worms could not maintain aerobic metabolism during long-term oxic sulfide exposure. Controls kept aerated before and during the experiments had succinate levels in the same range (Fig. 5).

Table 1. *Halicryptus spinulosus*. Concentration ($\pm$ SD) of sulfide and thiosulfate in hemolymph of worms immediately sampled on shipboard during different cruises, or after various periods in aerated seawater without sediment in the laboratory. Values of sulfur compounds are given in μM ; no. of samples in parentheses. tr: traces; nd: not detected; -: not determined

Sampling period ^a (wk)	18 Oct 1990	27 Nov 1990	2 Jul 1991	22 Nov 1991	31 Jan 1992
<i>In situ</i>					
0.5	Sulfide 342 $\pm$ 217	Sulfide 357 $\pm$ 243	Sulfide 445 $\pm$ 236	Sulfide 353 $\pm$ 232	Sulfide 86 $\pm$ 39
	Thiosulfate 69 $\pm$ 71 (9)	Thiosulfate 68 $\pm$ 59 (6)	Thiosulfate 21 $\pm$ 22 (10)	Thiosulfate 84 $\pm$ 74 (7)	Thiosulfate 26 $\pm$ 21 (10)
1	Sulfide 143 $\pm$ 25	Sulfide 172 $\pm$ 71	Sulfide 46 $\pm$ 28		
	Thiosulfate nd (5)	Thiosulfate nd (5)	Thiosulfate 14 $\pm$ 4 (4)		
2	Sulfide 61 $\pm$ 18	Sulfide 101 $\pm$ 43	Sulfide 48 $\pm$ 42		
	Thiosulfate nd (5)	Thiosulfate nd (5)	Thiosulfate tr (5)		
3	Sulfide -	Sulfide -	Sulfide 51 $\pm$ 30		
	Thiosulfate nd (5)	Thiosulfate -	Thiosulfate tr (5)		
5	Sulfide 80 $\pm$ 20	Sulfide 58 $\pm$ 38			
	Thiosulfate -	Thiosulfate nd (3)			
6					

^a *In situ*: immediately sampled; number indicates weeks after aerated incubation in the lab

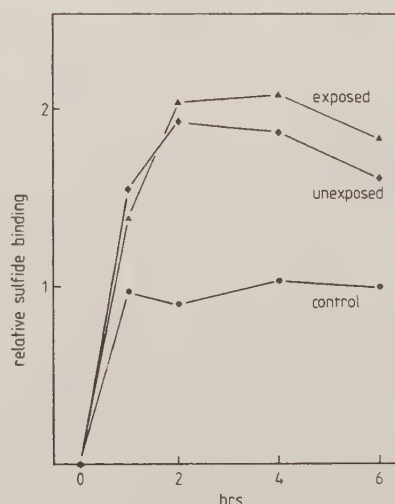


Fig. 4. *Halicryptus spinulosus*. Sulfide binding of buffered seawater (control, 22‰ S) and hemolymph of worms previously unexposed to sulfide and worms exposed for 10 d at 200 μM sulfide prior to binding experiments as function of dialysis duration. Experimental conditions: $9.5 \pm 0.5^\circ\text{C}$, 22‰ S

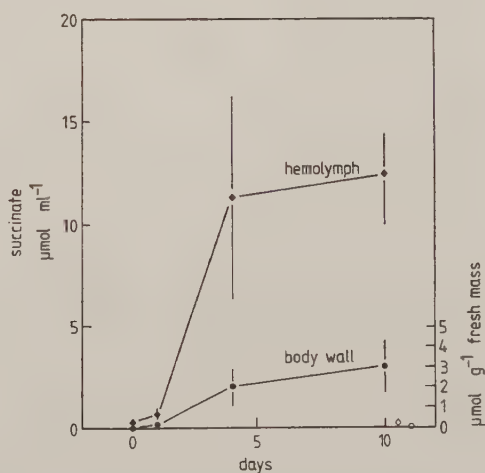


Fig. 5. *Halicryptus spinulosus*. Succinate accumulation $\pm$ SD in body wall tissue ($\blacksquare$) and hemolymph ($\bullet$) during oxic sulfide incubation. Measurements are means of 3 to 4 individuals (controls) and 5 to 11 individuals for incubated animals. Single data points (open symbols) after 10 d are control animals kept aerated without sulfide during the incubation experiment. Values are in $\mu\text{mol g}^{-1}$ fresh mass for body wall tissue and $\mu\text{mol ml}^{-1}$ for hemolymph. Experimental conditions: $9.5 \pm 0.5^\circ\text{C}$, 22‰ S

Activity of cytochrome c oxidase and catalase

Activity of cytochrome c oxidase was low in the hemolymph. *In vitro* inhibition of cytochrome c oxidase by sulfide from body wall tissue (K_i) was 1.05 ± 0.22 μM sulfide, while *in vivo* activity in body wall tissue of individuals exposed to 200 μM sulfide was ca 50 % of that of unexposed controls (Table 2).

In vitro inhibitory constants of catalase for sulfide (K_i) were in the same range for hemolymph (198 ± 25 μM) and body wall tissue (201 ± 32 μM). Activity of catalase in body wall tissue was not altered *in vivo* during 10 d of sulfide incubations (200 μM) (Table 2). Catalase activity in body wall tissue previously sonicated to strip off the mucus covering the worms showed no significant difference to that of untreated worms. Sodium azide, a specific catalase inhibitor, reduced the activity of the enzyme nearly completely. A concentration of 250 μM azide inhibited catalase activity in hemolymph by 86.4 ± 2.8 % ($n=5$), and a concentration of 1 mM inhibited the enzyme 94.4 ± 2.4 % ($n=3$). The activity of the enzyme from body wall tissue was almost entirely inhibited at 250 μM azide (97.8 ± 3.8 %, $n=3$).

Mitochondria

Different isolation procedures were tested. An isolation medium consisting of glycine and sucrose yielded maximal respiratory control rates (RCR). 2-oxoglutarate in the respiratory buffer was a prerequisite to measure respiration rates of *Halicyrtus spinulosus* mitochondria. RCRs with succinate (5 mM) as substrate were 1.72 ± 0.12 ($n=11$) with a maximum of 1.9. Mitochondrial preparations were cyanide-sensitive. Sulfide oxidation of the mitochondrial isolation

was fast in the lower sulfide range: up to 11.3 nmol sulfide mg^{-1} protein min^{-1} at 5 μM (i.e. 6.5 nmol sulfide in the assay) and up to 7.06 nmol sulfide mg^{-1} protein min^{-1} at 10 μM (i.e. 13.0 nmol sulfide in the assay). This rate might contain a certain fraction of an unspecific oxidation due to factors other than mitochondria. Sulfide inhibitory levels were 50 μM . More detailed mitochondrial sulfide oxidation characteristics need to be clarified in a further study.

DISCUSSION

When marine animals are confronted with environmental sulfide (its toxicity is attributed to the blocking of cytochrome c oxidase; National Research Council 1979), only limited defence responses are possible. Mobile fauna will be able to escape, unless the affected areas do not exceed small-scale ranges. Adult benthic macrofauna from soft sediments will be unlikely to escape into the water column, since these organisms generally have only very limited swimming capabilities. To live successfully in environments with the risk of frequent or regular exposure to sulfide, benthic macrofauna have to develop sulfide resistance as well as detoxification.

Adaptation to hydrogen sulfide can potentially take many forms in benthic infauna. Some mechanisms have been described but others doubtlessly remain to be elucidated. Mechanisms of sulfide resistance range from simple passive exclusion due to shell closure in bivalves to elaborate mitochondrial detoxification processes that produce ATP from sulfide oxidation (Powell & Somero 1985, O'Brien & Vetter 1990). *Halicyrtus spinulosus* possesses some mechanisms known from other invertebrates as well as some new processes.

Aerobic respiration in *Halicyrtus spinulosus* does

Table 2. *Halicyrtus spinulosus*. Activity of cytochrome c oxidase and catalase in control (no sulfide) and anoxic sulfide exposed (200 μM) worms. Values are means $\pm$ SD in U ml^{-1} for hemolymph or U g^{-1} fresh mass for body wall tissue. Unit definitions: 1 unit of cytochrome c oxidase converts 1 μmol of reduced cytochrome $\text{min}^{-1} \text{ml}^{-1}$ hemolymph or g^{-1} fresh mass of body wall tissue; 1 unit of catalase decomposes 1 μmol of $\text{H}_2\text{O}_2 \text{min}^{-1} \text{ml}^{-1}$ hemolymph or g^{-1} fresh mass of body wall tissue. 50 % inhibitory constants (K_i) are given in μM $\pm$ SD for sulfide. No. of samples are in parentheses. —: not determined

	Cytochrome c oxidase		Catalase	
	Hemolymph (U ml^{-1})	Body wall (U g^{-1} fresh mass)	Hemolymph (U ml^{-1})	Body wall (U g^{-1} fresh mass)
Unexposed controls	0.05 ± 0.02 (5)	0.64 ± 0.2 (10)	102.6 ± 69.1 (5)	454.7 ± 127.5 (14)
Sulfide exposed worms (200 μM) after:				
1 d	—	—	—	462.1 ± 274.9 (6)
8 d	0.03 ± 0.01 (5)	0.37 ± 0.15 (5)	—	—
10 d	—	—	—	343.2 ± 136.7 (12)
K_i for sulfide (μM)	—	1.05 ± 0.22 (5)	198 ± 25 (5)	201 ± 32 (5)

not appear to be resistant to the effects of sulfide. Both intact mitochondria and specific enzymes show sulfide sensitivity at levels comparable to other organisms (Powell & Somero 1986, Bagarinao & Vetter 1990). *H. spinulosus* mitochondria are involved in sulfide oxidation. As in other marine organisms (Powell & Somero 1986, Bagarinao & Vetter 1990, O'Brien & Vetter 1990) mitochondrial oxidation only works when sulfide concentration does not exceed a critical limit. When oxygen is available (as in the respiration chamber), mitochondria will oxidise sulfide. This process is cyanide sensitive. Preliminary studies on *H. spinulosus* mitochondria show that maximal oxidation rates are in the range of 5 to 10 μM sulfide, while inhibitory levels are in the range of 50 μM which is in agreement with other organisms tested so far (compilation in Bagarinao & Vetter 1990). ATP production in marine organisms using the proton potential generated by sulfide oxidation is generally low (Bagarinao & Vetter 1990, O'Brien & Vetter 1990). In the case of *H. spinulosus* the oxidation of sulfide primarily seems to be used as a detoxification process.

In this context it is tempting to speculate about an analogous mechanism known from brown adipose tissue in hibernating mammals and heater cells involved in keeping endothermy in Scombroideid fish. Mitochondria of these tissues are uncoupled from ATP production to solely generate heat (as quoted in Hochachka & Somero 1984, Block 1991). A similar ATP-independent mitochondrial sulfide oxidation clearly would facilitate sulfide detoxification. The involvement of mitochondria in sulfide detoxification in *Halicryptus spinulosus* is also proved by ultrastructural studies: mitochondria of epidermis and body wall tissue show altered electron densities caused by sulfide (Janssen & Oeschger 1992). Moreover there were electron dense inclusions in epidermal mitochondria after sulfide incubation suggesting the deposition of substances resulting from sulfide detoxification.

Halicryptus spinulosus has an *in vitro* sulfide inhibition constant (K_i) of cytochrome c oxidase of ca 1 μM . According to Bagarinao & Vetter (1990) this is in the upper range known for marine organisms. Catalase, another sulfide-sensitive enzyme with a metal-containing catalytic centre (National Research Council 1979), has a much higher *in vitro* inhibition constant, about 200 μM in body wall tissue and the hemolymph. *In vivo* activity of cytochrome c oxidase after 8 d of sulfide incubation (200 μM) is about 50% of oxic control worms, while catalase is not affected (Table 2). Striking differences for cytochrome c oxidase inhibition *in vitro* and *in vivo* are due to different pH conditions in the cuvette (assay carried out at pH 6.0) and during whole worm incubation (pH of ca 8.0 in the seawater). *In vitro* inhibition was tested by adding sulfide directly to the

assayed tissue homogenate of unexposed control worms, while *in vivo* inhibition was determined by measuring actual remaining activity in tissue homogenates after incubation (for a more detailed discussion see Bagarinao & Vetter 1990).

There is some evidence that both enzymes, cytochrome c oxidase and catalase, are mutually connected in their functioning. Morill et al. (1988) report catalase in thiobiotic meiofauna to be sulfide-insensitive like a bacterial pseudocatalase. In *Halicryptus spinulosus* a pseudocatalase is not found, since the enzyme is inhibited by azide, a specific catalase inhibitor. Nevertheless, a high sulfide concentration is needed to inhibit the enzyme *in vitro*, while no inhibition is detected in the range of realistic *in vivo* levels of sulfide (200 μM). Undiminished catalase activity in *H. spinulosus* is against the general acceptance that catalase is important especially in habitats where oxygen and its radicals can reach toxic levels. Catalase might be needed to protect *H. spinulosus* in the presence of sulfide, since inorganic reactions of sulfide can produce oxygen radicals and H_2O_2 (Millero 1986). Inhibition of cytochrome c oxidase by sulfide results in elevated levels of superoxide radicals and H_2O_2 due to increased amounts of reduced forms of respiratory chain components and tissue hypoxia may even aggravate this situation (Khan et al. 1990). In vertebrates hypoxia can activate xanthine oxidase which in the presence of sulfide stimulates the production of O_2^- (cf. Khan et al. 1990). Should sulfide thus produce increased amounts of toxic oxygen compounds, a maintained activity of catalase in the presence of sulfide clearly would be advantageous.

No marine animal is now able to exclude external sulfide from entering into the body (e.g. meiofauna: Powell et al. 1979; Crustacea: Vetter et al. 1987, Vismann 1991b; fish: Bagarinao & Vetter 1989). Under aerobic conditions *Halicryptus spinulosus* is able to keep sulfide concentrations in the body low for a certain time, even at high external sulfide concentrations (200 μM). Under this condition sulfide in body wall tissue increases slightly after 4 d probably due to a decreasing sulfide oxidation capacity. Hemolymphic sulfide concentration only increases somewhat after 10 d. High levels of thiosulfate, a non-toxic detoxification product of sulfide, are found in body wall tissue and hemolymph.

Halicryptus spinulosus is able to keep an internal aerobic sulfide oxidation for ca 4 d. The onset of anaerobic pathways, i.e. sulfide-induced anaerobiosis, is indicated after 1 d due to a slight succinate accumulation, a typical anaerobic metabolite. In the subsequent days the worms accumulate considerable amounts of succinate, indicating an elevated fraction of anaerobiosis. The recourse to anaerobic pathways goes

against the classical definition of anaerobiosis as being triggered by the absence of oxygen. Sulfide as a trigger of anaerobiosis in the presence of oxygen has been reported so far in the case of *Solemya reidi* (Anderson et al. 1990) and most recently in *Sipunculus nudus* and *Arenicola marina* (Völkel & Grieshaber 1992).

When the environment becomes anoxic and sulfidic, *Halicryptus spinulosus* appears to use a short-term defence to control influx of external sulfide. *H. spinulosus* differs from all previously studied organisms in its formation of black, acid-labile iron-sulfide interactions, which may produce Mackinawite-like (FeS) or Greigite-like (Fe₃S₄) compounds, and the ease in which it can apparently reverse this process. The conspicuous blackening of the worms is attributed to sulfide reacting with iron (mostly Fe²⁺) which is present in large amounts on the cuticle. Thus a first protection against sulfide is achieved (Oeschger & Janssen 1991). The effect of this mechanism is confirmed by ultrasonification. When the outer, iron-sulfide containing mucus is removed, body wall tissue contains less sulfide. A similar mechanism is discussed for internal iron deposits supposed to participate in sulfide detoxification in the gut of echinoderms (Buchanan et al. 1980, de Ridder et al. 1985) and in the mid-gut gland of an isopod (Vismann 1991b). An outer shield in *H. spinulosus* seems advantageous when the worms burrow in deeper sediment layers where they may encounter varying concentrations of sulfide (Fig. 1). A certain degree of blackening of the cuticle also occurs during oxic sulfide incubation. About 50 % of the incubated worms became black after 3 d. This outer shield is rechargeable as previously reported. Oxygen reverses the colour change (Oeschger & Janssen 1991). The black colour also disappears when treated with acidic solutions.

Such a striking colour change in a marine invertebrate related to sulfide exposure and its involvement in sulfide detoxification has not yet been reported. O₂-independent oxidation of sulfide mediated by iron ions is also reported for anoxic seawater (Millero 1991a, b). At the present we can only speculate about similarities of these mechanisms.

Sulfide oxidation to thiosulfate under anoxia is only of minor importance. At the beginning of the experiments a small increase of thiosulfate in body wall tissue and hemolymph was detected. We attribute this to an oxygen supply limited by the storage capacity of hemerythrin, the respiratory pigment of priapulids. Thus, other mechanisms must be effective. *Halicryptus spinulosus* binds some sulfide to a yet unknown hemolymphic-borne binding factor. Buffering of sulfide by binding should be another short-term defence, although a 2-fold sulfide-concentration capacity in *H. spinulosus* is moderate compared to a 6-fold one in

Escarpia laminata, a vestimentiferan worm (Cary et al. 1989a). Sulfide binding proteins have so far only been found in marine animals with endosymbionts (Arp et al. 1984, 1987, Cary et al. 1989a) and might also be present as an iron-protein complex in the mid-gut gland of *Saduria entomon* (Vismann 1991b). The hemolymphic binding factor of *H. spinulosus* explains a 2- to 3-fold accumulation of sulfide over external levels, which would be impossible according to the laws of diffusion. High hemolymphic sulfide levels (up to 80 µM) after 5 to 6 wk of aerated incubation (Table 1) or in controls (Fig. 3a) indicate that the binding factor releases sulfide very slowly. This is supported by the absence of thiosulfate after prolonged incubation (Table 1). Sulfide binding in *H. spinulosus* may result in a certain fraction of acid-volatile sulfide as reported for *Saduria entomon* (Vismann 1991b). This still has to be elucidated for the priapulid worm. In such a case elevated sulfide levels are attributed to a bound acid-labile fraction which does not harm the animals.

A distinct colour change of the hemolymph of *Halicryptus spinulosus* after ca 3 d of anoxic sulfide incubation indicates that the hemerythrin reacts with sulfide. Hemerythrin is known to contain a substantial amount of iron (Klotz et al. 1957), so that an iron-sulfide interaction seems likely. In contrast to hemoglobin, hemerythrin binds oxygen by changing its valence from Fe²⁺ to Fe³⁺ (Klotz et al. 1957, Klippenstein 1980). Our preliminary studies on the coelomic fluid show that the black component is associated in the erythrocytes and has a molecular weight > 10 kDa, when we used a centrifugation procedure that excludes molecules of this size. Thus we can rule out formation of a free iron-sulfide complex, which would have passed the membrane due to its molecular size. At this time we can only speculate on a binding to the hemerythrin since hemolymph regains its usual pinkish colour when oxygen is present. Our findings are in accordance with Schreiber et al. (1990), who reported a major hemolymph iron-containing constituent of ca 12 kDa with tightly bound iron. This binding is not disturbed by treatments of strong detergents, reducing agents or heat denaturation, and represents the respiratory pigment, i.e. hemerythrin, of the animals. Sulfide binding implies a release at a later time. Presently we do not know if the sulfide will be released when the pigment is reoxidised or if it is released as an oxidised form of sulfide. Presumably the oxygen-binding capacity will be destroyed by sulfide binding. It has yet to be elucidated if the sulfide binding means a beneficial adaptation or if it is a mere chemical interaction between sulfide and respiratory pigment.

Binding of sulfide may at least temporarily prevent mitochondria in *Halicryptus spinulosus* from being poisoned since these organelles are obviously important

in sulfide detoxification. But this may only work as a short-term protection depending on the oxygen storage capacity of the hemerythrin. A putative enzymatic sulfide oxidase activity separate from mitochondria has previously been reported (Powell & Somero 1985). Due to non-physiological assay conditions the method used to demonstrate such a specific enzymatic activity has been doubted (Bagarinao & Vetter 1990). So far there is no evidence for a specific enzyme and its physiological relevance. Spontaneous sulfide oxidation catalysed by metal ions (Chen & Morris 1972) may be a large portion of the 'sulfide oxidase' activities. Thus mitochondrial sulfide oxidation confirmed for the bivalve *Solemya reidi* (Powell & Somero 1986) and marine fish (Bagarinao & Vetter 1990) might be the only well-documented sulfide oxidation system at physiologically realistic conditions.

This study also suggests that anaerobiosis is involved in sulfide resistance. *Halicryptus spinulosus* has a remarkable anaerobic capacity (Oeschger 1990). Succinate accumulation during oxic sulfide incubation shows that the worms rely to an increasing degree on anaerobic metabolism. Obviously *H. spinulosus* has to switch to anaerobiosis when sulfide influx becomes too high for detoxification to keep up. Worms will be forced to passively survive this adverse environmental condition by becoming metabolically quiescent. Calorimetric studies prove an enormous metabolic reduction (Oeschger et al. 1992). Such a reduction will also be an advantage during elevated sulfide exposure. In *H. spinulosus* anaerobic glycolysis is not affected by the presence of sulfide over 10 d (Oeschger & Storey 1990). On the other hand one has to take into consideration that accumulating acidic anaerobic metabolites will cause a substantial drop in internal pH. Such a decrease intensifies sulfide toxicity. Thus the accumulation of acidic end-products might be an essential factor affecting long-term survival. At a physiological pH of ca 7.6 to 8.0 the toxic form of sulfide, the uncharged molecule H_2S , is present at 10 to 20% (APHA 1985). When pH drops, e.g. to 7.0, ca 50% of sulfide will be present in the uncharged form (H_2S) which will readily penetrate membranes. Even though glycolysis is not affected in *H. spinulosus*, an aggravation due to elevated sulfide influx with concomitant increase of undissociated toxic H_2S as a result of a decreasing internal pH seems to be unavoidable. During long-term sulfide exposure this may lead to fatal interferences with metabolic processes.

Whole animal model of sulfide control

The presented data allow an overall model of sulfide detoxification and resistance to be made in a marine

invertebrate from soft sediment. External sulfide is partly immobilised on the outer mucus barrier by precipitating iron-sulfides, made visible by blackening of *Halicryptus spinulosus*. When sulfide exposure prevails above the precipitation capacity, toxic sulfide entering the worm is oxidised to thiosulfate, the major detoxification product. Thiosulfate production depends on oxygen availability. When sulfide concentration exceeds a specific threshold, aerobic pathways are supplemented by an increasing fraction of fermentative ATP production.

Simultaneously or upon exhaustion of oxygen or detoxification capacity in mitochondria, a hemolymphic binding factor, which seems identical with hemerythrin, also limits free sulfide concentration. This process may help to keep mitochondria from being poisoned to a certain degree. Later the hemerythrin also blackens when obviously being involved in sulfide binding. When these mechanisms of sulfide control are overwhelmed by further sulfide influx, *Halicryptus spinulosus* switches entirely to anaerobic energy metabolism. This is to passively outlast sulfide. On return to oxic non-sulfidic conditions, worms regain their pale colour by reversible iron-sulfide splitting. *H. spinulosus* can reverse inorganic iron-sulfide formation and restore hemerythrin function. Further research should be directed to elucidating the nature of these protein-bound, iron-sulfur compounds and the biochemical mechanism of their reversal.

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Chromatophoromas and Related Hyperplastic Lesions in Pacific Rockfish (*Sebastes* spp.)

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ABSTRACT

Pacific rockfish were sampled from Cordell Bank, off central California, from 1985 to 1990. Hyperplastic and neoplastic lesions, involving dermal chromatophores, were observed in five species; yellowtail rockfish (Sebastes flavidus), bocaccio (S. paucispinis), olive rockfish (S. serranoides), widow rockfish (S. entomelas), and chilipepper rockfish (S. goodei). Yearly prevalences were highest, but static, in S. paucispinis, while prevalences in S. flavidus have risen steadily. The majority of lesions were black, but white, red, orange, yellow, and mixed color variants were also seen. Lesions were found in skin, fins, lips, gingiva, tongue, urogenital papilla, and in the conjunctiva and cornea of the eye. Flat lesions were consistent with either melanophore (black), erythrophore (red), or xanthophore (yellow) hyperplasia. Neoplastic lesions included melanophoromas, amelanotic melanophoromas, xanthophoromas, erythrophoromas, and mixed chromatophoromas. Electron microscopy did not reveal the presence of viruses and the etiology of the lesions has not been determined.

Pacific rockfish are ovoviviparous marine fish that are extensively fished. One of the most popular fishing areas is Cordell Bank, the northernmost sea mount in the California continental shelf. The bank is the primary site of ongoing rockfish recruitment studies by the National Marine Fisheries Service. Over the course of numerous sampling trips, pigmented lesions consistent with chromatophore hyperplasia and neoplasia (chromatophoromas) were observed in five species of rockfish: yellowtail rockfish

(*Sebastes flavidus*), bocaccio (*S. paucispinis*), olive rockfish (*S. serranoides*), widow rockfish (*S. entomelas*), and chilipepper rockfish (*S. goodei*).

Chromatophoromas are cutaneous pigment cell tumors that arise from dermal chromatophores normally present in skin. Chromatophoromas are common tumors and large epizootics have occurred in marine and freshwater environments. Species of marine fish involved include (1) croakers (*Nibea mitsukurii*) off the Pacific coast of Japan,¹ (2) deepwater redfish (*Sebastes mentella*) in the North Atlantic,² and (3) butterflyfish (*Chaetodon multicinctus* and *C. miliaris*) from the Hawaiian Islands.³

The purpose of this study was to characterize the gross, histologic, and electron microscopic features associated with pigmented lesions in rockfish sampled from Cordell Bank from 1985 to 1990. Prevalence and scoring (based on severity of hyperplastic and neoplastic melanophore lesions) data were determined for all species except *S. serranoides*. Selected lesions were processed for light and electron microscopy.

Yearly prevalences were consistently higher in *S. paucispinis*, with the highest prevalence, 38.6%, occurring in 1987 (Table 1). Prevalence in *S. flavidus* was initially low, but increased more than three-fold from 1985 to 1990. Melanophoromas were primarily found in *S. flavidus* and prevalence varied from 0% (1985) to 8.6% (1990). Xanthophore (yellow and orange) and erythrophore (red) lesions were only observed in *S. flavidus*. Prevalence of melanophore lesions was consistently higher in male versus female *S. flavidus* and *S. goodei*, but was nearly equal in *S. paucispinis*. The prevalence of all lesion types increased with age.

The average melanophore lesion score was significantly higher in *S. flavidus* (19.8%) compared with the other three species (10.5–10.9%).

TABLE 1
Prevalence of Hyperplastic and Neoplastic Pigmented Skin Lesions in *S. flavidus*, *S. paucispinis*, *S. entomelas*, and *S. goodei* Collected from Cordell Bank from 1985 to 1990

Year	% Prevalence (number of fish with lesions/number of fish examined)			
	<i>S. flavidus</i>	<i>S. paucispinis</i>	<i>S. entomelas</i>	<i>S. goodei</i>
1985	7.5 (7/94)	35.1 (13/37)	6.3 (1/16)	8.2 (4/49)
1986	11.3 (15/133)	29.0 (11/38)	5.3 (1/19)	16.7 (3/18)
1987	9.8 (15/153)	38.6 (17/44)	0.0 (0/8)	ND
1988	11.0 (12/109)	37.8 (14/37)	0.0 (0/2)	ND
1989	16.8 (17/101)	ND	ND	ND
1990	25.5 (56/220)	ND	ND	ND

ND = not determined.

Average scores for *S. flavidus* increased markedly with age, and males scored higher than females. There were minimal differences in lesion scores between male and female *S. paucispinis* or *S. goodei*, and no appreciable change in lesion scores as these fish aged. Melanophore lesions in *S. flavidus* had a dorsal and anterior distribution while the opposite was true for *S. goodei*. Melanophore lesions in *S. paucispinis* and *S. entomelas* were more severe ventrally.

Pigmented lesions in *S. flavidus* were found in the skin, fins, lips, gingiva, tongue, urogenital papilla, and in the conjunctiva and cornea of the eye (Fig. 1). The majority were black, but white, red, orange, yellow, and mixed color variants were also seen. The smallest lesions were round to irregular, flat foci that varied from 0.1 to 2 cm in diameter. In severely affected fish, foci coalesced to form large areas of melanosis. Raised masses, varying from 0.2 to 2 cm in diameter, were occasionally found. Masses were usually solid black, but other color variants were also occasionally seen. Lesions in *S. serranoides* were very similar to those in *S. flavidus* except that no yellow, orange, or red lesions were seen. Lesions in *S. paucispinis* were primarily found over the flanks, and were limited to flat foci of benign melanosis. Lesions in *S. entomelas* were similar to those in *S. serranoides*, and those in *S. goodei* similar to lesions in *S. paucispinis*.

Histologically, the smallest foci of melanosis were characterized by

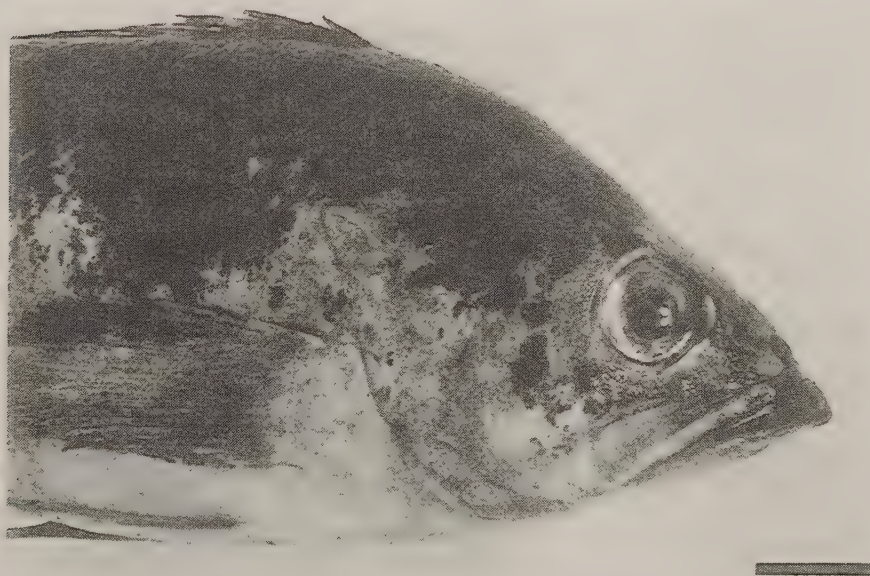


Fig. 1. *S. flavidus* with severe melanophore hyperplasia involving the dorsal aspect of the flanks, pectoral fin, lips, and conjunctiva of the eye. Bar = 2.5 cm.

hyperplasia of melanophores in the superficial dermis. Hyperplasia varied from mild to severe. Areas of severe hyperplasia often graded into small foci of dysplasia (mild to moderate disorganization and pleomorphism) and early neoplasia (accentuated disorganization, variability in pigmentation, and pleomorphism). All neoplasms with predominantly melanin bearing cells were classified as melanophoromas. Melanophoromas were composed of pleomorphic populations of stellate to spindle cells arranged into tightly packed, interweaving fascicles and whorling bundles (Fig. 2). The degree of pigmentation was highly variable and predominantly white tumors were classified as amelanotic melanophoromas. Xanthophoromas and erythrophoromas were not distinguishable from either each other or from amelanotic melanophoromas in routine HE sections and classification was based on the gross coloration prior to fixation. Yellow and orange tumors were classified as xanthophoromas and red tumors identified as erythrophoromas. Liver masses from one *S. flavidus* and gill masses from one *S. serranoides* were consistent with metastases.

Tissue for electron microscopy was only collected from *S. flavidus*. Melanophores were characterized by the presence of melanosomes, erythrophores by lipid, and xanthophores by lipid and pterinosomes. A few tumors contained widely scattered iridophores with reflecting platelets.

The gross, histologic, and electron microscopic features of pigmented

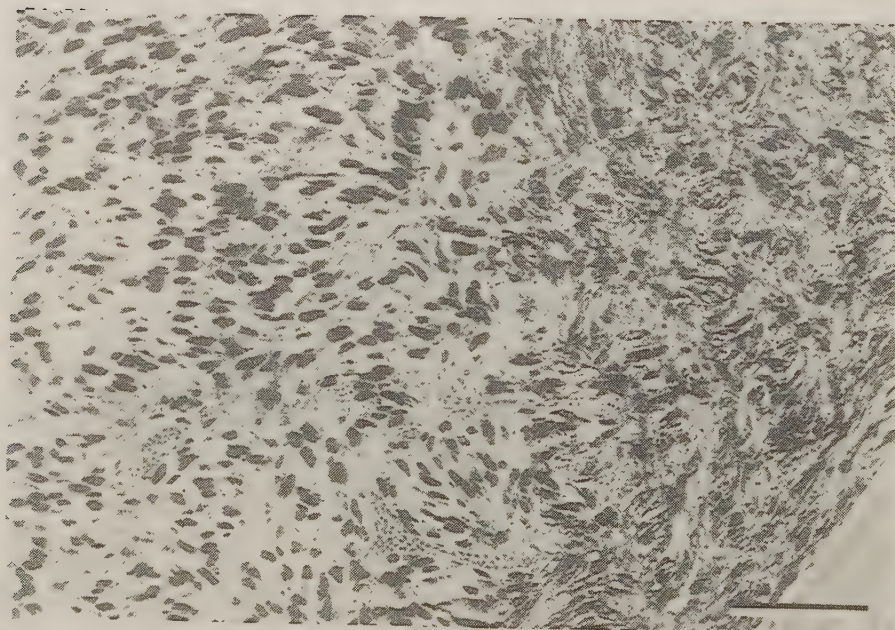


Fig. 2. Melanophoroma composed of a pleomorphic population of spindle cells heavily laden with melanin. Bar = 50 μ m.

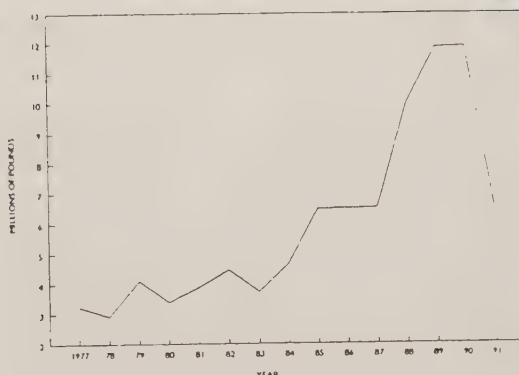
lesions in rockfish were all consistent with the diagnosis of chromatophore hyperplasia and neoplasia. Hyperplastic lesions are likely precursor lesions of chromatophoromas and progression appears to occur stepwise from mild melanophore hyperplasia to severe hyperplasia, dysplasia, and eventual neoplasia (melanophoroma). Xanthophore and erythrophore hyperplasia probably precede formation of xanthophoromas and erythrophoromas. The etiology is unknown, but interest is currently focused on waters surrounding the Farallon Islands (south of Cordell Bank) which were used as a radioactive and toxic waste disposal site from 1946 to 1970. Approximately 47 500 barrels of low-level radioactive waste and 47 800 barrels of unspecified toxic waste were dumped at three sites.⁴ Limited sampling has already revealed high levels of chlorinated hydrocarbons (DDTs and PCBs) in sablefish (*Anoplopoma fimbria*) and Dover sole (*Microstomus pacificus*),⁵ and trace levels of plutonium-239 in *S. flavidus*. Efforts are underway to expand the study area to include the Farallons in order to establish a more definitive link between the cutaneous lesions in rockfish and possible exposure to carcinogenic compounds in the environment.

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California commercial landings of thornyheads, 1977-1991.

THORNYHEADS

History of the Fishery

The two species of thornyheads (genus *Sebastolobus*) in California waters are most abundant at depths where Dover sole and sablefish live. Shortspine thornyhead (*S. alascanus*) are taken by the commercial fishery at depths as shallow as 600 feet, and it is likely that thornyhead landings were predominately shortspine during the early years when the fishery operated in relatively shallow water. Longspine thornyhead (*S. altivelis*) were probably not landed in large quantities until later when the fishery expanded into deeper water. Although there are consistent differences between the two species, distinguishing between them can be difficult under field conditions. Landings and other data for each species may, therefore, be less reliable than data for thornyheads as a group.

From 1953 to 1969 total thornyhead landings in California ranged from just over 3,000 pounds to 900,000 pounds. Thornyheads became common as incidental catch when California trawlers began fishing intensively for Dover sole in the early 1970's. In 1970, total thornyhead landings in California exceeded one million pounds for the first time and averaged 2.8 million pounds per year from 1970 to 1979. Thornyhead landings increased to an average of six million pounds per year from 1980 to 1989.

Thornyheads were originally marketed as a rockfish product (usually fillets) in domestic markets. Increased landings during the 1980's were the result of increased prices and demand for thornyheads, primarily as a headed and gutted product exported to Japan. Changes in species composition and markets for thornyheads occurred during the late 1980's as the fishery moved into deeper water to harvest longspine thornyheads. As export markets developed, prices paid to fishermen more than doubled from \$0.17 to \$0.40 per pound (all prices and revenues in 1989-equivalent dollars). Gross revenues for thornyheads landed in California rose from \$576,000 in 1980 to \$5,425,000 in 1990 as the result of increased prices and landings. The relative value of thornyheads in the groundfish fishery also increased during that time. Revenues from thornyheads were only 12 percent of total revenues for the deepwater fishery (thornyheads, sablefish, and Dover sole) during 1980, but increased to 39 percent by 1990.

Fishing for thornyheads is typically by bottom trawl and longline gear in relatively deep water (1,800 to 3,000 feet) on sand or fine sediment. Fishermen report that there are areas where shortspine and longspine thornyheads are found together and other areas where longspine thornyhead predominate. Most of the thornyheads landed in California are taken in the Eureka, Fort Bragg, and Morro Bay areas. Few thornyheads are taken south of Point Conception. With the 4.5-inch mesh in cod ends currently used in the commercial trawl fishery, thornyheads become vulnerable to bottom trawls at about five to seven inches in length and at an age of about eight to nine years. Thornyheads are seldom taken by gill nets or in the recreational fishery because of the depths at which they live.

Thornyheads are managed by the Pacific Fishery Management Council under the Groundfish Management Plan. Shortspine and longspine thornyheads are managed as a group because of difficulties in separating the two species during fishing and in the landings. Catch quotas for thornyheads were first used in the fishery during 1990.



Shortspined thornyhead, *Sebastolobus alascanus*.

Status of Biological Knowledge

Thornyheads belong to the same family (Scorpaenidae) as the rockfishes (*Sebastes* spp.) but are distinguished from them in having more dorsal and head spines, in losing their swim bladder at the time they settle to the bottom, and in spawning gelatinous egg masses. Shortspine thornyheads grow to larger size and are found in shallower water than longspine thornyheads. The adults of both species are major components of the assemblage of fishes of the continental slope where they co-occur over a broad depth range of 1,600 to 4,900 feet. Both

species have special enzymatic adaptations which allow metabolic activity despite the high pressure and low temperature at the depths where they live.

Shortspine thornyhead are found at depths of about 100 to over 5,000 feet along the west coast of North America from northern Baja California to the Bering Sea and across the north Pacific to the coast of Japan. It is not known if separate stocks exist. Off California, shortspine thornyhead spawn during late winter and early spring. Males off Alaska may spawn at about 6.5 inches in length (estimated age 5). About half of all females off California are sexually mature at 8.25 inches in length (estimated age 13) and almost all are sexually mature at 13.5 inches (estimated age 28). Estimates of ages are based on counts of growth rings in thin-sectioned otoliths. This approach has not yet been validated for either species of thornyhead, so all ages must be regarded as estimates. A female may release as many as 400,000 eggs annually in gelatinous egg masses that float to the surface. Larvae free themselves from the egg when about 0.25 inch in length and transform to juvenile fish at about 0.75 inch. Larvae and young juveniles are pelagic for 14 to 15 months and settle to the bottom when about one inch long during January to June of the year after they hatch. Juveniles settle in shallow water along the upper boundary of their habitat and move to deeper water as they grow. They spend the rest of their lives closely associated with the bottom.

Shortspine thornyheads can grow to 30 inches and may be quite long-lived. It is particularly difficult to determine the age of older individuals, but recent estimates indicate that the maximum age of shortspine thornyheads off California may be in excess of 100 years.

Shortspine thornyheads in Alaska are known to eat crustaceans, crabs, worms, clams, octopus, sea cucumbers, and fish. Longspine thornyheads feed primarily on polychaetes and small crustaceans.

Longspine thornyheads are found from Cape San Lucas, Baja California to the Aleutian Islands in water from about 1,000 to over 5,000 feet deep. It is not known if separate stocks exist.

Like shortspine thornyheads, longspine thornyheads spawn in the late winter and early spring. Half of the females are sexually mature at about 7.5 inches in length (estimated age 14) and most are mature at 8.75 inches (estimated age 18). A female may produce as many as 100,000 eggs annually, which, like the eggs of the shortspine thornyhead, are released in gelatinous egg masses that float to the surface. Two to four batches of eggs may be spawned each year. Larval fish are pelagic after hatching and transform into juveniles during July to December. Young juveniles are pelagic for as long as 20 months and begin settling to the ocean bottom when about two inches long. Settling starts during the summer of the year after they hatch. Juvenile longspine thornyheads settle on deeper bottoms than do shortspine thornyheads, with newly settled juveniles occupying a broad range of depths from approximately 1,600 to 4,000 feet. There does not appear to be a tendency for individuals to move deeper as they grow. Longspine thornyheads grow to a maximum length of 15 inches. Their maximum age is probably at least 45 years.

Status of Population

Recent estimates from research trawl survey data indicate that total biomass of thornyheads off California north of Point Conception is between 34,100 and 151,800 tons. Most of the total biomass (14,400 to 101,200 tons) probably consists of longspine thornyheads. The extent to which fishing has reduced abundance of thornyheads is not known since no information about historical biomass levels is available.

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Abstract.—Mortality due to retention of lobsters in derelict traps was evaluated over a 2-year period using two approaches. First, a string of eight empty, single-chamber, plastic traps was deployed at 40 m depth off Oahu, Hawaii, and monitored periodically by scuba during a 6-month period in 1990. The traps were stable and remained intact despite adverse oceanic conditions. Numerous entries and exits of lobsters were recorded. For the second test, the ability of lobsters to exit traps was tested in a series of field and laboratory trials of trap strings stocked with Hawaiian spiny lobster *Panulirus marginatus* and slipper lobster *Scyllarides squammosus*. The number of lobsters that died in stocked traps was less than 4% of the test population and differed significantly from zero only in the laboratory evaluation (χ^2 5.42, P 0.02). The two species exited similarly; however, the pattern of exits in laboratory and field tests differed significantly (χ^2 23.889, P 0.03). All lobsters exited within 56 days in a pattern generally approximating an exponential decline. Our evidence suggests that little direct mortality of lobsters is due to the inability to exit traps, and consequently ghost fishing by these traps is not considered a problem for spiny and slipper lobsters.

Evaluation of ghost fishing in the Hawaiian lobster fishery

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Continued fishing by lost traps has become the focus of increasing concern by both fishery managers and scientists. The recent trend for trap fisheries to replace their degradable traps with designs made from more persistent synthetic materials has heightened the seriousness of possible ghost fishing by such unrecovered traps. Ghost fishing has been defined as the continued fishing of irretrievable gear (Smolowitz 1978). Such a definition fails to distinguish between permanent entrapment and temporary occupation of a trap (e.g., for feeding or shelter). Mortality occurring in abandoned traps should be measured to assess the impact of ghost fishing on a particular fishery.

The phenomenon of ghost fishing has been observed in a wide range of trap fisheries with diverse trap designs (e.g., High 1976, Pecci et al. 1978, Smolowitz 1978, Paul 1983). Despite this attention, few studies have effectively assessed the ghost fishing problem for any species. The more rigorous evaluations rely on continued underwater field observations of simulated lost traps (Breen 1990). With this method, mortalities have been clearly demonstrated in temperate fisheries in which animals were unable to exit traps fitted with nonreturn entrance devices. Features such as spring-loaded doors and slick plastic entrance chutes effectively reduce the ability of some animals to exit actual and simulated lost traps, resulting in reported mortalities of 26–55% (High 1976, Miller 1977, Breen 1987). Conventional wooden,

two-chamber or “parlor-type” traps designed for the American lobster *Homarus americanus* have produced mortalities of 12–25% (Sheldon and Dow 1975, Pecci et al. 1978, Smolowitz 1978).

Ghost fishing poses a potential risk to at least some trap fisheries, and such a risk requires assessment for each species and trap configuration. Tropical lobsters have been largely neglected in the controlled evaluation of mortality by ghost traps. Isolated anecdotal reports of tropical lobsters found in lost traps (Sutherland et al. 1983) and tank studies made to date (Paul 1983) do little to predict realistic, long-term effects of lobsters interacting with modern traps in the field.

Hawaii’s lobster fishery targets two species, Hawaiian spiny lobster *Panulirus marginatus* and slipper lobster *Scyllarides squammosus*. A laboratory study by Paul (1983) used California parlor-type traps made of wire to determine the effectiveness of escape vents in releasing undersized Hawaiian spiny lobster. Paul (1983) suggested that ghost fishing might occur in these traps and recommended that the Hawaiian fishery consider incorporating degradable escape panels to facilitate the escape of adult lobsters. By 1985 the fishery had adopted a more cost-effective molded-plastic trap design as the standard gear. Degradable panels have not been included.

In 1989 the Hawaiian lobster industry reported that more than 1 million traps were set in the Northwestern

Hawaiian Islands (NWHI); an estimated 2000 of these traps were unrecovered (Landgraf et al. 1989). The annual accumulation of lost plastic traps on the banks where commercial trapping occurs must be considered a potential hazard to the lobster stocks. No field studies have been done on the interactions between lost traps and the adults of the two target lobster species. The objectives of this study were to (1) evaluate the persistence of lost commercial traps under field conditions, (2) estimate retention of target species in plastic traps with bait depleted, and (3) assess mortality of lobsters unable to exit traps.

Methods

Study sites

The prohibitive cost of prolonged, ship-supported diving operations in the NWHI dictated that all field experiments be conducted at Oahu. Sites close to the windward shore of Oahu provided appropriate depths (30–40 m) and habitat consistent with the NWHI commercial banks. The area is known to harbor exploitable numbers of the lobster fishery's target species. Its heavy seas, strong bottom surge, and swift currents (Bathen 1978) might mimic NWHI conditions and thus could test the stability of lost traps. Traps placed in such rough conditions, without surface markers, were unlikely to be disturbed by fishermen and other recreational users.

Trap stability and faunal interactions

A string of eight empty traps was deployed in a linear orientation from February to July 1990. The selected area afforded two types of adjacent habitat—high-relief rugose bottom, and hard relatively-flat bottom—allowing comparisons of trap stability and use by lobsters in the different environments. Individual traps were set 10 m apart, four on high-relief bottom and four on adjacent even bottom. The molded-plastic traps (Fig. 1) used in the study were a standard commercial model employed throughout the commercial fishery in Hawaii (Fathoms Plus Marine Implementation, P.O. Box 6307, San Diego, CA 92106). Each trap consisted of a single chamber with two side entrances and was weighted with about 10 kg of lead, as is conventional in the

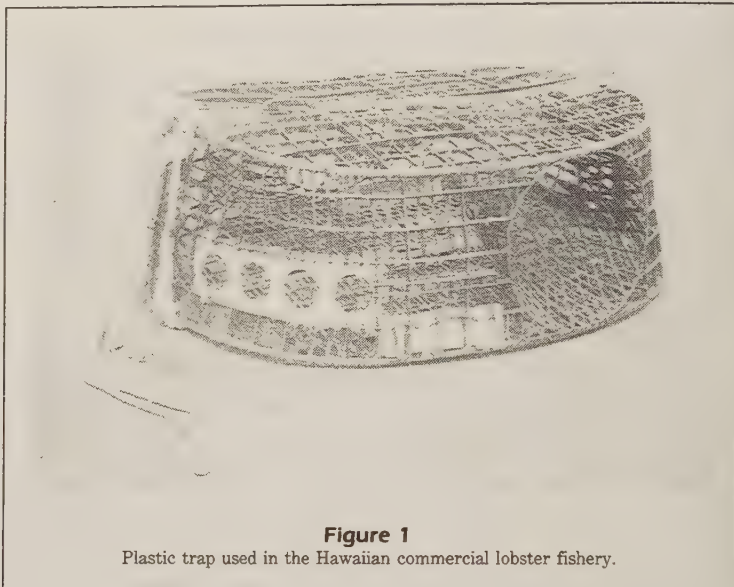


Figure 1

Plastic trap used in the Hawaiian commercial lobster fishery.

fishery. Traps remained in place over a 6-month period. They were observed monthly by scuba divers during three dives conducted at 48-hour intervals. Physical condition, movement, and contents of the traps were noted on each dive, along with general observations of the surrounding area. The monthly censuses recorded the initial presence of lobsters from the surrounding study site and any exits or entries over the following 4 days. The area in and under the traps was examined for exoskeleton remnants that might indicate molting or mortality. One additional trap with its hinge pins removed was deployed on flat bottom near the trap string to mimic a trap with corrodible hinge pins that had deteriorated.

Trap stocking experiment

In the summers of 1990 and 1991, traps of the same type (Fig. 1) were deployed in the field and laboratory, and stocked with spiny and slipper lobsters from the NWHI to evaluate their ability to exit and the extent of mortality. Prior to the traps being stocked, lobsters had spent 3–8 days in transit in continuously-flushing shaded bait wells where they were fed daily. Mean carapace lengths were 87.6 mm ($N = 96$, range 67.4–121.7 mm) for spiny lobster, and 83.3 mm ($N = 96$, range 50.1–99.7 mm) for slipper lobster. Antennae were tagged with color-coded, plastic, self-locking, electrical ties to permit visual identification of individuals without their being handled during the experiment. Molt stage

of lobsters prior to their deployment in traps was determined using Lyle's (1982) adaptation of Drach's (1939) staging technique.

In the field test, 128 tagged lobsters were placed by divers in 4 strings of 8 unbaited traps each (2 spiny and 2 slipper lobsters per trap). Two strings were placed on and around high-relief substrate, one in summer 1990 and the other in summer 1991; two strings were placed on relatively-flat hardbottom, at least 300m from any relief that could provide lobsters shelter, in summer 1991. The contents of the traps were checked every 48 hours until all tagged lobsters had exited or died.

In the laboratory trials, 64 additional tagged lobsters were placed in 16 traps (2 spiny and 2 slipper lobsters per trap) in a large, shaded, outdoor concrete tank. Throughout the tank, food and other suitable shelter were provided outside the traps to encourage exiting. Contents of the traps were monitored daily, and any lobsters found outside the trap in which they were originally stocked were removed from the tank. Lobster death totals in the laboratory (where predation could not occur) and in the field were compared in an attempt to separate losses by predation from other mortality (e.g., starvation, conspecific aggression) in the field.

This study employed a modified experimental cohort design to examine the effects of multiple categories (replicate, habitat type, species) on exiting by lobsters. The design permits cross-classified categorical analysis to be applied (Fienberg 1987). Using chi-square tests, comparisons were made between replicates, habitat types, and species in a systematic order. Categories were collapsed or pooled when justified by the lack of significant differences (Siegel and Castellan 1988).

Results

Trap stability and faunal interactions

Estimated seas of 4–6 ft and currents of 1–2 knots were common at the study site. They produced no observable effect on the physical integrity of the plastic traps. Movement of traps across the substrate was not detected, despite frequent observations of the interconnecting groundline actively moving in the bottom surge. The two halves of the trap without hinge pins shifted 2 cm apart. Over the 6-month period, the traps became encrusted with sessile organisms, including bryozoans, corals, and fish eggs. Occasionally adult fish larger than the opening of the escape vent were found in the traps; however, most of these departed through the trap entrance as a diver approached.

Adults of both spiny and slipper lobsters local to the surrounding study site entered the traps. Of the 12 such occurrences of lobsters recorded during the 6-month survey, 7 lobsters left before the last inspection of the monthly observation period, indicating that they did not occupy the traps

for more than 30 consecutive days. Three lobsters were observed entering and exiting within the same 48-hour observation period. Nine of the 12 lobsters were found in traps on even bottom.

One dead spiny lobster comprised the only mortality observed within the 6-month field evaluation. Postmortem examination and the presence of lobster debris in the area around the trap suggested death by predation. Sightings of known predators such as octopus, eels, jacks, and sharks were routine. Large eels often occupied the traps, occasionally with lobsters.

Trap stocking experiment

Molt-stage evaluation indicated that 27% of the spiny lobsters and 1% of the slipper lobsters were in the premolt stage at deployment. Mortality was limited to seven spiny lobsters, five in the laboratory and two in the field. All of these lobsters were in premolt stage at deployment and died during or shortly after molting. Despite the limited mortality, the number of deaths in the laboratory trials differed significantly from zero

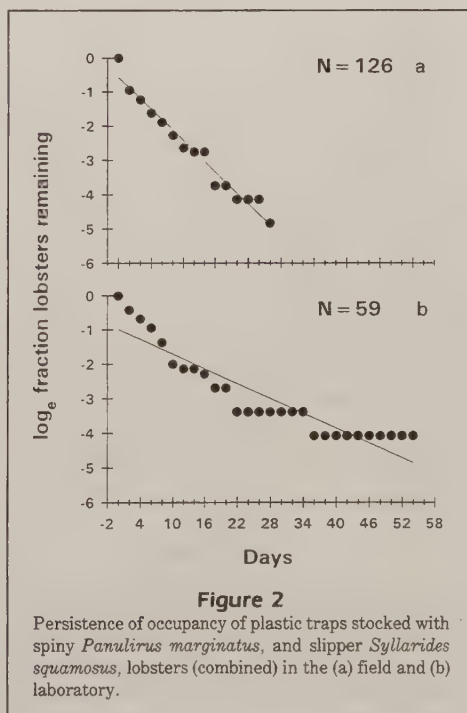


Figure 2

Persistence of occupancy of plastic traps stocked with spiny *Panulirus marginatus*, and slipper *Syllarides squamosus*, lobsters (combined) in the (a) field and (b) laboratory.

(χ^2 5.42, P 0.02). This was not true for the field trials (χ^2 2.06, P 0.15), and mortalities in the laboratory and field were significantly different (χ^2 4.74, P 0.03). Consequently, the two test situations were evaluated separately, with all animals that died excluded from the trap-occupation analysis.

Contingency tables were used to test for differences in the exit distributions for various groups of the data (Fienberg 1987). Within each species, the distributions of exits were first compared between replicate trap strings within the same habitat type and were found not to be significantly different (spiny lobster—high relief, χ^2 3.22, P 0.07; even substrate, χ^2 10.00, P 0.19; slipper lobster—high relief, χ^2 3.33, P 0.07; even substrate χ^2 9.52, P 0.02). Therefore, the distributions of exits for the two replicates were pooled within each habitat type. Within each species, exits were then compared for the effect of the two habitat types and were found not significantly different (spiny lobster— χ^2 10.81, P 0.01; slipper lobster— χ^2 4.53, P 0.03). The distributions of two habitat types were then pooled within each species, and exits of the two species were not significantly different (χ^2 16.93, P 0.08). Consequently, the distributions of the two species in all field trials were combined (N 126 lobsters after 2 early mortalities) for further comparisons.

Within each species, exits observed in the tank were compared with the field data pooled by replicate and habitat type and were not significantly different (spiny lobster— χ^2 14.42, P 0.01; slipper lobster— χ^2 13.63, P 0.09). Exits of spiny and slipper lobsters in the tank were not significantly different (χ^2 11.55, P 0.32), and the data were subsequently pooled (N 59 lobsters after 5 early mortalities). A comparison of exits of all lobsters in the tank (pooled) and all lobsters in the field (pooled) showed a significant difference (χ^2 23.889, P 0.03).

Half of the 126 spiny and slipper lobsters stocked in the field and 33% of the lobsters stocked in the laboratory exited within 48 hours after being placed in the traps. Ninety percent or more of the exits in both tank and field trials occurred within the first 16 days. All field animals had left by day 30, and all laboratory animals by day 56. The overall exit pattern of the lobsters suggested an exponential model. The data were fitted to the log-transformed exponential function

$$\ln_e (N_t/N_0) = bt,$$

where N_t is the number of lobsters remaining after time t from N_0 lobsters initially stocked. The parameter b was estimated with a log-linear regression procedure for the field traps ($b = -0.16/\text{day}$; r^2 0.992, SE 0.284, $P < 0.001$) and for the laboratory traps ($b = -0.094/\text{day}$, r^2 0.961, SE 0.632, $P < 0.001$; Fig. 2).

Stocked spiny and slipper lobsters exited and re-entered field traps in at least 13 instances; 6 lobsters returned to the same trap. One spiny lobster was observed exiting three traps within 6 days.

Discussion

Trap stability

The lack of structural damage and appreciable movement of the plastic traps in the field contrasts with the popular opinion of experienced fishermen that lost traps break up and roll off the banks into waters beyond the depth range of lobsters. Fishermen routinely report movement of trap strings as a result of powerful swells moving across the commercial banks. Despite the frequently observed movement of the groundline by swells at the Oahu study site, it is likely that the study site does not fully duplicate the power of the long-term swells common in the NWHI. Lost traps may not shift on the bottom as much as actively fished traps. Buoys and interconnecting polypropylene line provide additional lift and resistance to water motion; therefore, fully rigged strings of traps are more likely to move than isolated traps severed from the groundline. A 1990 systematic diving survey of 33 sites around 2 of the prominent NWHI commercial lobster fishing banks revealed only 2 mangled derelict traps (F. Parrish, unpubl. data). The failure to locate large amounts of lost gear may be partly explained by this survey being incidental to other work. Total gear losses in 1989 averaged about 1 trap/nm² over the total estimated area of the lobster fishing grounds (Landgraf et al. 1989). Lost gear could be heavily concentrated in a few of the more intensively fished areas that the survey may have missed.

A trap manufacturer (Fathoms Plus Marine Implementation) has made available a corrodible pin which is intended to allow the halves of plastic traps to eventually fall apart once the pin deteriorates. The fact that our pinless trap remained relatively intact for 6 months in the field suggests that the synthetic plastic clips on the trap roof will continue to hold the trap together, especially for fisheries conducted in calmer seas.

Mortality and movement of lobsters

Seven deaths among the 192 spiny and slipper lobsters within the 56-day study represent low mortality when compared with the natural mortality estimates from the fishery population modeling by Haight and Polovina (1992). Extrapolation of the experiment's percentage of mortality from 2 months to 1 year (22%) is close to half the fishery's annual estimated natural mortality (40%). The fact that only animals that began the trials

in premolt condition died suggests that lobsters at this stage are less fit. The probability that this mortality would occur only with premolt individuals by chance alone is <0.001 (Agresti 1990). Increased vulnerability to a poor physical environment, conspecific aggression, or predation have been associated with molting (Conan 1985). It seems likely that the higher percentage of spiny lobster in premolt stage accounts for some of the difference in mortality between spiny and slipper lobsters.

The significantly higher mortality observed in the laboratory compared with the field does not support the idea that undetected predation substantially affected the field results. The relatively low absolute level of total mortality suggests that such predation is probably minimal at the field site. However, with mortality being higher in the laboratory than in the field, no estimate of predation is possible.

More than twice as many deaths were observed in the laboratory as in the field, even though the field trials involved twice as many lobsters and three times as many were in the premolt stage. This suggests a less healthy or fit laboratory population, which is consistent with the significantly slower exit of pooled species from traps in the laboratory versus in the field. Aspects of the laboratory environment (e.g., water quality, lighting, diet) may have degraded the physical condition of the lobsters or affected their behavior, inhibiting their exit, or providing less inducement to leave the traps than that encountered in the field. It seems likely that our field assessment provides a better estimate of natural exit patterns.

With a study design similar to ours, Munro (1974) examined the rate of fish exiting unbaited traps. His theoretical model suggests that the number exiting per day may be a fixed fraction of the current trap occupancy, and that catch eventually reaches an asymptote when trap entrances are balanced by exits. Our number of stocked lobsters declined approximately exponentially, approaching zero asymptotically. However, the total occupancy of traps declined daily until it reached a low and varying level at which exits were roughly matched by entrances of lobsters. This final, low level of trap occupancy at the end of the stocking experiment seems consistent with native occupancy observed during the monthly field monitoring.

In our stocking tests, some individuals likely left a trap and reentered it undetected between censuses, particularly in the field test where the observation interval was 48 hours. Based on independent probabilities of exit and entry estimated from our field data, the theoretical joint probability of such reentry was as high as 0.06, and probably about 12 individuals left and reentered the same trap undetected during the full 26-day field stocking experiment.

Conclusion

Our results indicate that spiny and slipper lobsters are not restrained by lost molded-plastic traps for periods long enough to cause serious harm. There is no evidence that such lost traps result in increased mortality. The absence of any apparent trap-induced mortality and the low incidence of identifiable in-trap mortality due to predation suggest that ghost fishing by these traps contributes little to the total mortality of the population. Such traps, when unbaited and intact, may best be considered short-term artificial shelters that lobsters enter and exit occasionally, more or less at will.

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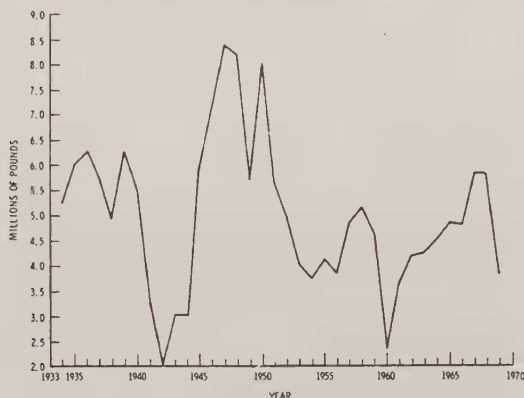
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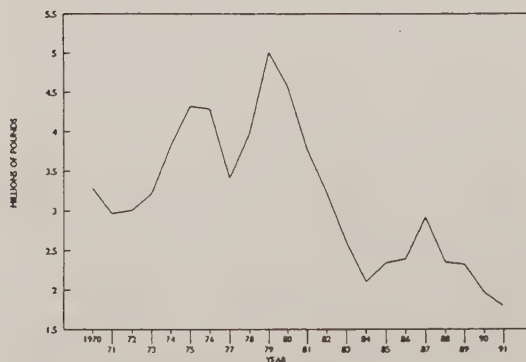
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abundant in the landings because they tend to be longer and heavier than the males. Fishing for English sole can be done by relatively small vessels because of the shallow water in which this species is found. Very little is taken by commercial hook and line or by gillnet, and it is not an important species for recreational fishing.



California commercial landings of English sole, 1933-1969.



Commercial landings of English sole, 1970-1991.

ENGLISH SOLE

History of the Fishery

English sole (*Pleuronectes vetulus*) has been commercially important since the introduction of the first trawl net, the paranella, in San Francisco in 1876. The use of trawl nets made the catch of "sole" species one of the leading categories of fish landed in California, and English sole was the leading flatfish in that group until Dover sole took first place in 1949. Since then, English sole has been second in pounds landed except for 1970-1972, when petrale sole was second. The peak year for English sole was 1929, when 8.7 million pounds were caught off central California and at new fishing areas off Fort Bragg and Eureka. Annual landings during the past 10 years have averaged just under three million pounds, mostly from grounds off the Eureka and San Francisco areas. Little is taken commercially south of Point Conception.

English sole are fished primarily by trawling in water 120 to 900 feet deep on sandy bottoms. They become vulnerable to the commercial fishery at three years of age (10 inches), but four- to eight-year-old fish (11-17 inches) predominate landings because markets request fish of at least 11 inches in order to produce reasonable size fillets. Female fish are often more

English sole is a desirable fish for the market and restaurant trade, primarily as a filleted product, but landings are affected by market demands and abundances of other flatfish and roundfish. Currently there are landings restrictions on certain rockfish and deep-water complexes of fish, and processors may request English sole from the fishermen to supplement total landings. Notwithstanding, landings of English sole have not increased since the implementation of restrictions on other fish. Demand for English sole is also affected by availability and price of imported fish products.

Status of Biological Knowledge

English sole range from San Cristobal Bay, Baja California to northwest Alaska in water as deep as 1,800 feet. Fish tend to move to deeper water in the winter and shallower water in the summer, and fishing effort follows these movements.



English sole, *Pleuronectes vetulus*.

Tagging studies in California, Oregon, Washington, and British Columbia show that, although there is little overall migration, small seasonal north-south movements probably occur, and some fish have been found to move in excess of 200 miles. Analysis of tag returns also suggest that four separate stocks are found in California: south of Point Conception, Point Conception to Bodega Bay, Monterey to Eureka, and Eureka to southern Oregon. The overlap in areas is a result of apparent north-south movement of the stocks. Some seasonal intermingling between stocks probably also occurs.

Female English sole are usually mature at three years (10 to 14 inches), while males mature at two (8 to 11 inches). Spawning occurs over sand and mud-sand bottoms at depths of 200 to 360 feet from September to April, although some spawning probably occurs in all months. In California peak spawning occurs from December through February, with annual variations in timing apparently related to water temperature. Each fish probably spawns only once per year. A three-year-old, 12-inch female releases approximately 150,000 eggs, while a 10-year-old, 17-inch fish will release almost two million. Egg diameter is approximately 0.04 inch. Fertilized eggs are buoyant when first released, but shortly before hatching they begin to sink into the water column.

When the eggs hatch, in four to 12 days, the larvae are approximately 0.1 inch long. Typically the larvae are in the mid-water column but sink deeper as they approach metamorphosis. During development, the larvae can be carried towards shore on upper-level water currents. Spawning and development during times of rapid plankton growth may result in good recruitment. During their pelagic phase of six to 10 weeks, the larvae grow to about 0.75 inch, then settle to the bottom and metamorphose to the adult benthic body form. After metamorphosis, and for the first year of life, juvenile English sole are found in shallow bays and estuaries and feed all the way up to the intertidal zone. Juveniles are found in sand, mud, and eelgrass habitats. The population density of juvenile English sole in estuaries is several times higher than on the open coast; however, it is not known how important estuaries are to survival of juvenile English sole. In southern California the shallow open coast may be more important as juvenile habitat than it is further north. As the fish grow they tend to move to deeper water.

The largest recorded English sole, from British Columbia, was 22.5 inches, and 21-inch fish have been taken in California. The oldest recorded age is 22 years. English sole are aged by counting the annual rings on the interopercular bone.

While in the estuary and nearshore shallow-water environment, juveniles feed on copepods, the palps of segmented worms, siphons of small clams, brittle stars, and other small invertebrates. At the end of their first year of life (about five inches) most juveniles have moved to offshore waters. Adult fish are seldom found in estuaries. They are opportunistic feeders eating shallowly burrowed or surface-active prey such as worms, small crustaceans, clams, and occasionally small fish, crabs, and shrimp. Adults can also dig into the sediment to reach deeper prey.

The English sole is capable of interbreeding with the starry flounder producing an intergeneric hybrid called the hybrid or forklime sole or flounder.

Status of Population

Little information is available to estimate the status of the English sole stock in California. Catch-per-unit-of-effort data exist but are complicated by the multiple species aspect of trawl fishing. Analysis of catch information for the late 1970's suggests that stocks are at levels that produce maximum sustainable yield. Currently there is no quota on the English sole fishery, but landings are monitored and populations continually assessed for signs of biological stress. The fishery is currently managed by the Pacific Fishery Management Council through gear regulations such as mesh size for trawl nets.

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Batch fecundity of *Sardina pilchardus* (Walb.) off the Atlantic Iberian coast

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ABSTRACT

Sardina pilchardus is a serial spawner releasing several batches of eggs per spawning season. The Hydrated Oocyte Method was used for the first time to estimate sardine fecundity on the Atlantic Iberian coast in 1988. The mean batch fecundity of the Atlantic Iberian sardine in March/April 1988 was 30 227.3 (standard error = 1 342.6) and the mean relative fecundity (number of hydrated oocytes per gram of female weight) was 426.54 (standard error = 18.95). The sardines' relative fecundity was higher than that of other clupeoid species. Sardine batch fecundity (F) was expressed as a linear function of ovary-free weight (W) based on both Portuguese and Spanish fecundity data: $F = -1\,184.7 + 443.26\,W$.

Key words: Batch fecundity, sardine, Iberian Peninsula.

RESUMEN

Fecundidad parcial de *Sardina pilchardus* (Walb.) de las costas atlánticas de la península Ibérica.

La especie *Sardina pilchardus* es un reproductor del tipo múltiple, por tanto, realiza varias puestas parciales en cada periodo reproductivo. En el año 1989 se utilizó por primera vez en las costas atlánticas de la península Ibérica el Método de Ovocitos Hidratados para el cálculo de la fecundidad de esta especie. El valor medio de la fecundidad parcial de la sardina atlántica de la península Ibérica calculado en marzo y abril de 1988 fue 30 227.3 (error = 1 342.6) y el valor medio de la fecundidad relativa (número de ovocitos hidratados por gramo de peso de hembra) fue 426.54 (error = 18.95). Este valor es más alto que el determinado para otras especies de clupeidos. La fecundidad parcial de la sardina (F) se expresa como una función lineal del peso vivo de las hembras sin ovario (W) basada en los datos obtenidos por Portugal y España: $F = -1\,184.7 + 443.26\,W$.

Palabras clave: Fecundidad parcial, sardina, península Ibérica.

INTRODUCTION

Fulton (1898) reported that before spawning, ovaries take up a fluid of low specific gravity and considerably increase in size (hydration process). Hydrated oocytes are microscopically distinguishable from the rest of oocytes in the ovary, and can be easily counted. Hunter and Goldberg (1980) developed the Hydrated Oocyte Method to determine batch fecundity of the northern

anchovy, *Engraulis mordax*. Fecundity estimates were only based on hydrated females caught a few hours before spawning, because hydrated oocytes can be easily separated from all other oocytes in the ovary for oncoming spawning. The total number of hydrated oocytes in the ovary corresponds to female batch fecundity. The Hydrated Oocyte Method is advantageous because it is accurate, and considerably reduces the time required to obtain fecundity estimates

(Hunter, Lo and Leong, 1985). In sardine, the increase of ovary volume after hydration may attain 264 % (Andreu, 1955), and hydrated eggs are easy to identify; thus, we chose the Hydrated Oocyte Method to determine the batch fecundity of sardine. This paper presents our experience of using this method to estimate the fecundity for *Sardina pilchardus*.

MATERIAL AND METHODS

Sardine were collected off the Atlantic Iberian coast by Portuguese and Spanish research vessels during a joint cruise undertaken in March/April 1988. Just after they were caught the sardines' body cavities (from anus to pectoral fins) were opened, and sex was determined. Ovary-free (Spain) and gutted (Portugal) female bodies were immediately frozen. Excised ovaries were preserved; the fixative used was:

- 4 % buffered formaldehyde solution (Hunter, Lo and Leong, 1985) (Spain).
- Bodian's AAF (Lillie and Fullmer, 1976) (Portugal) modified according to the following formula:

• Alcohol 50 %	65 ml
• Formalin 40 %	32 ml
• Glacial acetic acid	13 ml

Because fecundity estimates should be given in terms of live wet weight, correction coefficients to convert frozen fish weight to wet weight were needed. A number of 300 fish were used to calculate live wet weight and frozen weight after two months, and the value of correction coefficients estimated was used to estimate the live wet weight of all sample fish. The correction coefficients were computed from samples collected from commercial catches in Portuguese waters and from pelagic trawls executed during the Egg Production Method (EPM) survey in Spanish waters. The total fecundity and the corrected ovary-free fish weight, an estimated live wet weight, were analyzed to model the relationship between fish weight and total fecundity.

In order to analyze the hydrated oocyte distribution between left and right ovaries

and between lobes of the same ovary, we took four ovarian tissue subsamples from fish sampled in Spanish waters: one at the center and the other near one ovary edge, in both ovarian lobes. A total of 206 ovary tissue samples were examined. As to Portuguese samples, three ovarian tissue subsamples were taken from each ovary: one at the center and the other two at about one-third of the distance from each edge of only one ovarian lobe, and a total of 114 ovary tissue samples were examined. Egg number per unit ovary weight was calculated for each tissue subsample. Analysis of variance used to test differential distribution of hydrated oocytes inside the ovary and in between lobes was carried out separately for each country.

All the ovaries were histologically examined to detect postovulatory follicles. Their presence was an indication that spawning had been initiated, and that some hydrated oocytes had probably already been released. In such cases, ovaries were not used in fecundity estimates.

From each fish sampled, three tissue samples were examined. From each subsample, an estimated total oocytes was computed as the number of hydrated oocytes per g times the wet gonad weight. The batch fecundity estimate was the average of three estimated total hydrated oocytes (Hunter, Lo and Leong, 1985). As total fecundity increases with fish weight, batch fecundity was determined as a function of female weight, i.e., $EY = f(W)$, where W is the ovary-free wet weight. Ovary-free fish weight was used to prevent upward bias in weight, as females with hydrated oocytes temporarily weigh more than the average female (Hunter, Lo and Leong, 1985).

Simple linear regression was first fitted to the batch fecundity and fish weight data from each of the two countries separately. An analysis of covariance was performed to determine whether the adjusted mean batch fecundities (for a given ovary-free female weight) from the two countries were similar. If so, then data from both countries would be combined to evaluate the batch fecundity-fish weight relationship.

Several regression models for fitting batch fecundity and ovary-free weight data were established. All models included egg

number per batch (F) and ovary-free weights (W) recorded for each female sampled in Portuguese and Spanish waters. In addition to the fecundity-fish weight relationship, we also examined the fecundity-fish age relationship, using Portuguese data for comparison purposes.

RESULTS, DISCUSSION AND DISCUSSION

A total of 126 sardines with hydrated ovaries were collected during the EPM cruise (37 from Portugal and 89 from Spain). Hydrated oocytes were preserved with either formalin or Bodian's AAF modified. The resulting distinct characteristics of hydrated eggs are presented in table I. The correction factors used to convert frozen fish weight and preserved ovary weight to live fish weight and wet ovary weight were also

tissue samples per fish would be necessary if the variance within the ovary was high compared to the variance around the regression line (Hunter, Lo and Leong, 1985).

A weighted analysis of covariance was used to compare the adjusted batch fecundity for the average ovary-free fish weight between the two countries (table V), where the weight is the inverse of variance¹. The analysis of covariance indicated that the adjusted batch fecundity from the two countries was not different, at 0.05 level of significance ($F = 0.02$, with $d.f. = 1\ 123$). The adjusted batch fecundity for fish of 25.86 g (a weighted average ovary-free wet weight) was 10 308.54 for Portugal and 10 146.63 for Spain. Thus both Portuguese and Spanish data sets were used to establish a representative regression model of batch fecundity for female weight on the Atlantic-Iberian coast. A weighted least squares regression was used to model the fecundity and fish

Table I.—Effects of two different fixatives on hydrated oocytes.

Tabla I.—Efectos sobre los ovocitos hidratados de los dos diferentes líquidos conservantes.

<i>Preservative solution</i>	<i>Morphological characteristics of the hydrated oocytes</i>
4 % buffered formaldehyde	— large size — wrinkled appearance (yolked but nonhydrated oocytes usually retain their smooth contour) — translucence (nonhydrated oocytes are relatively opaque)
Bodian's AAF modified	— large size — unwrinkled contour — translucence apperaranace similar to unfertilized planktonic eggs — yolk granules visible

computed for both countries (table II). We also examined the effect of location of hydrated oocytes within ovaries and the effects of right and left ovaries on egg density. The analysis of variance indicated no significant difference in egg density within ovaries and between ovaries at 0.05 level of significance (tables III and IV). Thus, tissue samples from any location, from any one ovary, should give an unbiased egg density estimate. We took three tissue samples from each fish for modelling sardine batch fecundity and fish weight relationship. More

weight relationship (fig. 1) (Draper and Smith, 1981 in Hunter, Lo and Leong, 1985):

$$F = -1184.7 + 443.56 \cdot W^1$$

where F is the batch fecundity and W is the ovary-free wet weight.

¹ The variance was computed as follows: A simple linear regression of batch fecundity on fish weight was obtained for each country and residuals were obtained. Fish were grouped by 10 g increments and the variance of the residuals within each group was computed.

Table II.—Correction factors determined by each country (fW: frozen fish weight; gW: gutted fish weight, and fWov: preserved ovary weight).

Tabla II.—Factores de corrección calculados por cada país (fW: peso del pez congelado; gW: peso eviscerado, y fWov: peso del ovario fijado).

	<i>Spain</i>	<i>Portugal</i>
Wet fish weight	1.0559 (fW)	1.044 (fW)
Total fish weight	—	—0.568 + 1.127 (gW)
Wet ovary weight	0.991 (fWov)	0.852 (fWov)

Table III.—Effect of location of ovarian tissue samples from sardine on the number of eggs per unit sample weight (g), using Spanish data. Effects evaluated by taking tissue samples from two positions (middle, I and edge, II) and both from 103 right and 103 left ovaries.

Tabla III.—Efecto de la situación de las muestras de ovocitos del ovario de sardina, sobre el número de huevos muestreado por unidad de peso (g), con datos españoles. Efectos calculados para dos posiciones (centro I y extremo II) y para 103 muestras en cada uno de los ovarios, derecho e izquierdo. En un ovario sólo se realizaron dos muestras.

MEAN N.º EGGS/g OF OVARY									
Position of sample in ovary	RIGHT OVARY			LEFT OVARY			BOTH		
	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n
I	2080.6	58.42	52	2143.5	64.38	52	2112.0	43.36	
II	2060.9	55.26	51	2092.9	60.85	51	2076.6	40.86	

TWO-WAY ANALYSIS OF VARIANCE OF EGGS/g OF OVARY TISSUE				
SS due to	df	SS	MS	F
Right vs. left ovary	1	113806.28	113806.28	.620
Position within ovary	1	63066.12	63066.12	.344
Interaction	1	12303.82	12303.82	.067
Residual	202	37073891	183534.11	
Total	205	37264681		

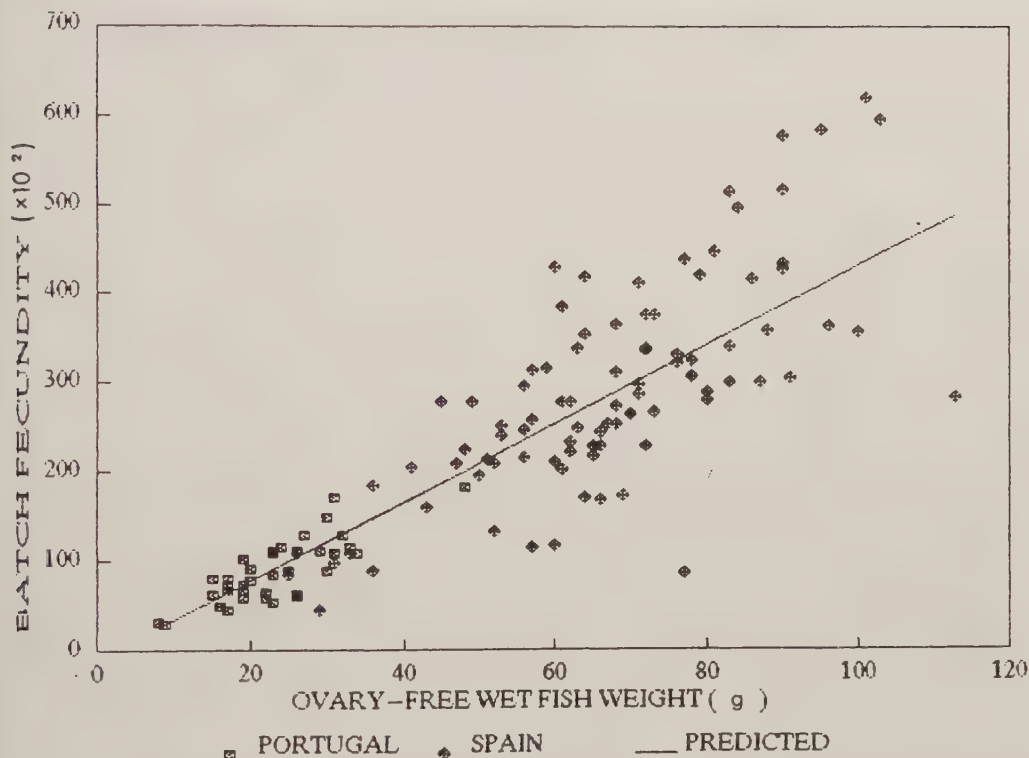


Fig. 1.—Linear regression of batch fecundity ($\times 10^2$) of *Sardina pilchardus* on the ovary-free wet fish weight (g). Data were from Portugal and Spain waters off the Atlantic Iberian coast.

Fig. 1.—Regresión lineal entre fecundidad parcial ($\times 10^2$) de *Sardina pilchardus* y el peso vivo de las hembras sin ovario. Los datos, aportados por Portugal y España, corresponden a las costas atlánticas de la península Ibérica.

The mean batch fecundity was estimated from equation (1) by replacing W with the mean ovary-free fish weight from the survey, which was converted from the mean fish weight based on a fish weight and ovary-free fish weight equation given in García *et al.* (1992). The mean batch fecundity estimate of *Sardina pilchardus* was 30 227.3 (standard error = 1342.6). We also computed the mean relative fecundity estimate as the mean fecundity divided by the mean ovary-free fish weight (426.53, standard error = 18.95). When compared with other clupeoids (Lo, Alheit and Alegre, 1986; Alheit and Alegre, 1988), *Sardina pilchardus* produces more eggs per body weight than most other Clupeidae (187–413/g) (table VI).

Although linear regression was chosen to model fish weight and fecundity relationships, two nonlinear models were also presented for comparison purposes (table VII).

Expression of batch fecundity by age group was based only on Portuguese data (table VIII). Comparison of linear regression models indicated that fecundity increases more rapidly with age than with fish weight (tables VII and VIII). This may be a consequence of the age data used, mainly composed of younger sardines (age group 1 and 2) which present higher growth rates than older ones.

Comparison of linear regression models indicated that fecundity increases more rapidly with age than with fish weight (tables VII and VIII). This may be a consequence of the age data used, mainly composed of younger sardines (age group 1 and 2) which present higher growth rates than older ones.

Table IV.—Effect of location of ovarian tissue samples from sardine on the number of eggs per unit sample weight (g), using Portuguese data only. Effects evaluated by taking tissue samples from three positions (middle, I and at one-third distance from each edge, II and III).

Tabla IV.—Efecto de la situación de las muestras de ovocitos del ovario de sardina, sobre el número de huevos muestreado por unidad de peso (g), con datos portugueses. Efectos calculados para tres posiciones (centro I y a un tercio de los extremos II y III).

MEAN N.º EGGS/g OF OVARY			
Position	$\bar{x}$	S.E.	n
I	2733.3	115.37	38
II	2060.9	136.63	38
III	2734.2	114.46	38
Total			114

TWO-WAY ANALYSIS OF VARIANCE OF EGGS/g OF OVARY TISSUE					
SS due to	df	SS	MS	F	Sig. lev.
Between groups	2	5220	2609.92	0.005	0.9954
Within groups	111	63380485	570995.36		
Total	113	63385705			

Table V.—Analysis of covariance for the effect of country on the adjusted mean batch fecundity. The covariate is ovary-free fish weight.

Tabla V.—Análisis de covarianza del efecto de los países sobre el ajuste de la fecundidad parcial media. Covariante es peso de las hembras sin ovario.

ANALYSIS OF COVARIANCE FOR DEPENDENT VARIABLE - FECUNDITY						
Source	Sum of squares	D.F.	Mean square	F	Tail prob.	Regression coefficients
Country	0.01749	1	0.01749	0.02	0.8995	
fw	246.866008	1	246.86608	230.51	0.000	4.4628
Error	131.72915	123	1.07097			

ADJUSTED MEANS FOR DEPENDENT VARIABLE		
	Portugal	Spain
Fecundity ($\times 10^2$)	103.08544	101.46636

Table VI.—Relative fecundity of various clupeoid fish species. (Adapted from Alheit, 1988.)

Tabla VI.—Fecundidad relativa de varias especies de clupeidos. (Adaptada de Alheit, 1988.)

Group	Species	Area	Relative fecundity	n	Authors
Clupeidae	Sardines	California	263	91	MacGregor, 1957
		Perú	283		Lo, Alheit and Alegre, 1986
	<i>Sardinops sagax</i>	Chile	255	168	Retamales and González, 1983
	<i>Sardinops ocellatus</i> ⁽¹⁾	SW Africa	265	127	LeClus, 1987
	<i>Sardina pilchardus</i>	Portugal	427		Present paper
Sardinella	<i>Sardinella brasiliensis</i>	Brazil	356	23	Isaac-Nahum <i>et al.</i> , 1988
	<i>Sardinella aurita</i>	Senegal	400		Connand, 1977
Sprat	<i>Sprattus sprattus</i>	Kiel Bay, Baltic	232	46	Heidrich, 1925
	<i>Sprattus sprattus</i> ⁽²⁾	Southern North Sea	413	41	Alheit, 1987
Others	<i>Clupea bentincki</i> ⁽³⁾	Chile	350	126	Mújica and Rojas, 1984
	<i>Herklotsichthys quadri maculatus</i>	Hawaii	236	46	Williams and Clarke, 1983

⁽¹⁾ For a female of 120 g. ⁽²⁾ At peak of spawning. ⁽³⁾ Recalculated.

Table VII.—Models used to express the relationship between female batch fecundity (Y) and female ovary-free weight (X).Tabla VII.—Modelos usados para expresar la relación entre fecundidad parcial (Y) y peso de las hembras sin ovario (X).

Model	a (se)	b (se)	MSE (10^{-5})	R^2 ⁽³⁾
$Y = a + bX$	-2291 (1488)	471.15 (24.94)	50.1	0.74
$Y = a + bX$ (weighted)	-1184.7 (535.9)	443.26 (17.45)	0.0106	0.83
$Y = a \cdot X^b$	252.48 (85.6)	1.12 (0.77)	50.0	0.74
$Y = e^{(a + bX)}$	8.9614 (0.0914)	0.0185 (0.0012)	58.4	0.70

⁽³⁾ R^2 is computed as the regression sum of squares divided by the total sum of squares.

Table VIII.—Models used to express the relationship between female batch fecundity (Y) and female age (X).Tabla VIII.—Modelos usados para expresar la relación entre fecundidad parcial (Y) y la edad de las hembras (X).

Model	a (se)	b (se)	MSE (10^{-6})	R^2
$Y = a + bX$	3 081 (806.85)	3 711.88 (470.089)	4.7	0.64
$Y = a + X^b$	6 696.24 (392.818)	0.68884 (0.0742)	4.2	0.68
$Y = e^{(a + bX)}$	8.66856 (0.8061)	0.25835 (0.0343)	6.2	0.52

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The spawning frequency of sardine, *Sardina pilchardus* (Walb.), off the Atlantic Iberian coast

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ABSTRACT

Oocyte development for *Sardina pilchardus* was established, and a histological classification of postovulatory follicle aging was developed from the examination of laboratory-spawned sardine. The established criteria were compared with those used for field collections taken during the Portuguese-Spanish joint Egg Production Method Survey (March-May 1988).

The fraction of mature females with postovulatory follicles, < 48 hours old, for the Iberian Peninsula was 0.14 (standard deviation = 0.0122), indicating that the mean interval between spawnings was approximately 7 days.

Key words: Spawning fraction, sardine, Iberian Peninsula.

RESUMEN

Frecuencia de puesta de sardina, *Sardina pilchardus* (Walb.), en las costas de la península Ibérica.

Se determina para la especie *Sardina pilchardus* el proceso del desarrollo ovocitario, y se clasifica histológicamente las diferentes edades de degeneración de los folículos postovulatorios por medio del estudio de gónadas de sardinas inducidas artificialmente a la puesta. Los criterios establecidos se comparan con los utilizados en muestras procedentes de las campañas de investigación para el desarrollo del Método de Producción Diaria de Huevos, realizadas por Portugal y España conjuntamente (marzo a mayo de 1988).

Se determina la fracción de hembras maduras que ponen por día mediante el estudio de los folículos postovulatorios de edad menor de 48 horas, que en el caso de la sardina de la península Ibérica es de 0.14 (desviación típica 0.0122), indicando que el intervalo medio entre dos puestas parciales es de 7 días aproximadamente.

Palabras clave: Fracción de hembras reproductoras, sardina, península Ibérica.

INTRODUCTION

Sardine (*Sardina pilchardus*) spawn more than once within a spawning season, and present more than one mode of advanced oocytes in their active ovaries (Andreu and Pinto, 1957). Estimation of spawning frequency is essential to understand the reproductive biology of a species with an indeterminate annual fecundity. The standing stock of more advanced oocytes gives no

indication of annual fecundity, because new batches are regularly recruited from small unyolked oocytes during the spawning period (Hunter and Macewicz, 1985).

Spawning frequency and the number of eggs released per spawning are required to estimate annual reproductive effort or fecundity, and are also needed to find out how these variables are related to population size and age structure (Hunter, Macewicz and Sibert, 1986).

The first histological work on *Sardina pilchardus* was done by Pinto and Andreu (1956). By histological examination, they found that the fish length at which the sexual glands of sardine first become outlined within the coelom was 37 mm. They also found that sexual differentiation took place in larvae 45 mm long, and ovaries were completely organized in those 100 mm long.

This paper aims to describe the postovulatory follicle reabsorption process and to establish a criteria for determining follicle age in order to estimate the spawning frequency of *Sardina pilchardus*.

MATERIAL AND METHODS

The material used in this paper is based on sardine samples collected by pelagic and bottom trawls during the Daily Egg Production Method (DEPM) survey held March to May 1988 by both Spain (R/V Cornide de Saavedra) and Portugal (R/V Noruega) (see tables I to V), and on sardine spawned in captivity (12 °C, February 1989).

Adult sardines captured by commercial purse seine during February 1989 were induced to spawn in the laboratory using the technique developed by Leong (1971). Three sardines spawned: one, 215 mm total length (L_t), was sacrificed 19 h after spawning; the second, 175 mm L_t , died 34 h after spawning; and the third, 180 mm L_t , died 61 h after spawning. Their ovaries were used as a first approach for the establishment of the histological criteria for determining the age of sardine postovulatory follicles. The validated classification system obtained was compared with that developed for the sea-caught females sampled during the DEPM survey.

Ovaries were removed and preserved in two different fixatives: Spain, 10 % buffered formalin (NBF) according to Hunter (1985); and Portugal, acid-alcohol-formalin (AAF) after Bodian (1937) in Lillie and Fullmer (1976), modified. The second fixative presented a high penetration coefficient; even large ovaries were well and homogeneously fixed. Harris' hematoxylin and eosin (H & E) staining procedure was used.

Histological characteristics of oocytes

Oocyte development and maturation in teleosts has been frequently subdivided into many stages. Hunter and Macewicz (1985) proposed a simpler histological classification system in which they combined the stages defined by former authors into four oocyte stages (unyolked, partially yolked, yolked and hydrated). We adopted this classification system for our work.

Unyolked Oocytes

In this stage, smaller oocytes are distributed in an orderly manner along the ovarian septa and have no cytoplasmic inclusions. They generally exhibit a polygonal section, sometimes rectangular and rarely spheric or oval. They present a basophilic cytoplasm, very densely stained with hematoxylin, and a voluminous central nucleus containing several nucleoli. Later on, oocytes present two different chromatic affinities (H & E): the inward zone (perinuclear cytoplasm) lightly stained, and the outward zone, which presents the same staining as the smaller oocytes. These two groups of oocytes were classified by Andreu (1951) as α phase ($<100 \mu\text{m}$). Macroscopically, they present a transparent appearance which corresponds to the immature or inactive stage (stage I in Andreu and Pinto, 1957).

Subsequently, the oocytes become more spherical, and the perinuclear zone less defined than in the previous groups. In oocytes with a larger diameter, the zona radiata appears between the oocyte and the growing follicle as a thin, faint eosinophilic membrane. The follicle begins to be visible in oocytes with diameters between 100 and 150 μm (Andreu, 1951) as a thin layer of elongated cells (the beginning of the granulosa cells).

Partially Yolked Oocytes

This stage involves oocytes in which vitellogenesis (yolk deposition) begins, determining a different staining reaction; the cytoplasm basophilic appearance progressively decreases. Oocytes become more spherical, and oil vacuoles migrate to the neighbor-

hood of the nucleus and become more voluminous. Delicate striations appear in the zona radiata. The follicle layer is thicker, and the differentiation between thecal and granulosa cells is clear.

Yolk deposits begin to form near the central cytoplasmic area as small spherules, while the remaining cytoplasm has a basophilic appearance. As vitellogenesis proceeds, larger globules spread into the oocyte limits when yolk granules reach the perinuclear zone.

Yolked Oocytes

Oocytes are more voluminous, and they all contain yolk granules throughout the region between their periphery and the perinuclear zone. Vitellogenesis continues, and yolk granules vary to large globules. Oil vacuoles fuse at the proximity of the nucleus to form a single oil droplet. The zona radiata stretches and the follicle now corresponds to a thin membrane that surrounds the oocyte. Yolked oocytes macroscopically present a yellowish appearance.

Hydrated Oocytes

The final stage of vitellogenesis corresponds to hydration, a rapid uptake of the fluid by the follicle (Fulton, 1898, in Hunter and Macewicz, 1985). Hydration seems to begin when the nucleus has completed its migration to the animal pole and, simultaneously, yolk globules begin to fuse, forming yolk plates. The enlargement of the oocyte, which reaches about 1 mm diameter, causes the flattening of the thecal and granulosa cells as well as the thinning of the zona radiata.

Spawning Frequency

Two methods have been developed for measuring the spawning rate of multiple spawning fish (Hunter and Macewicz, 1985). Sardine spawning frequency was determined using the postovulatory follicle method. This method requires a division of the processes of deterioration and resorption of

the follicles into a series of distinct histological stages, each one with a specific age assigned (Hunter and Macewicz (1985)).

Since in 1988 no validation system existed to classify sardine postovulatory follicles by age, the histological characteristics of the deteriorating follicles, the time of sampling, and the average population peak spawning time was used to assign ages to the postovulatory follicles. In February 1989 an artificially induced spawning technique was used to obtain the time after spawning, i.e. age, of sardine postovulatory follicles. These ages were then used to confirm the histological criteria applied to the postovulatory follicles of sea-caught females sampled in the DEPM survey during 1988 (Olmedo *et al.*, 1990).

The classification system for *Sardina pilchardus* postovulatory follicle ages is described below. Results for Portugal and Spain are shown in tables VI to X. Despite the relatively few numbers of immature females present in the samples in two western Cantabrian stations, immature females represented almost 72 % of total females sampled (table VII), which may be related to a differential distribution of immature and mature shoals during the spawning period.

The incidence of alpha-atresia increases in more degenerated postovulatory follicles.

Age 0-h postovulatory follicles

Since no laboratory female was sacrificed at the moment of spawning, the description of age 0-h follicles corresponds to ovaries with both new postovulatory follicles and hydrated eggs from sea-caught females. Cord-like cell layers of collapsing follicles form loose folds or loops at ovulation (fig. 1).

Age 19-h postovulatory follicles

After spawning, fully collapsed postovulatory follicles form a much more tightly folded or looped structure. It is relatively large, irregular in shape, and has an irregular lumen. The thecal cell layer is very thin

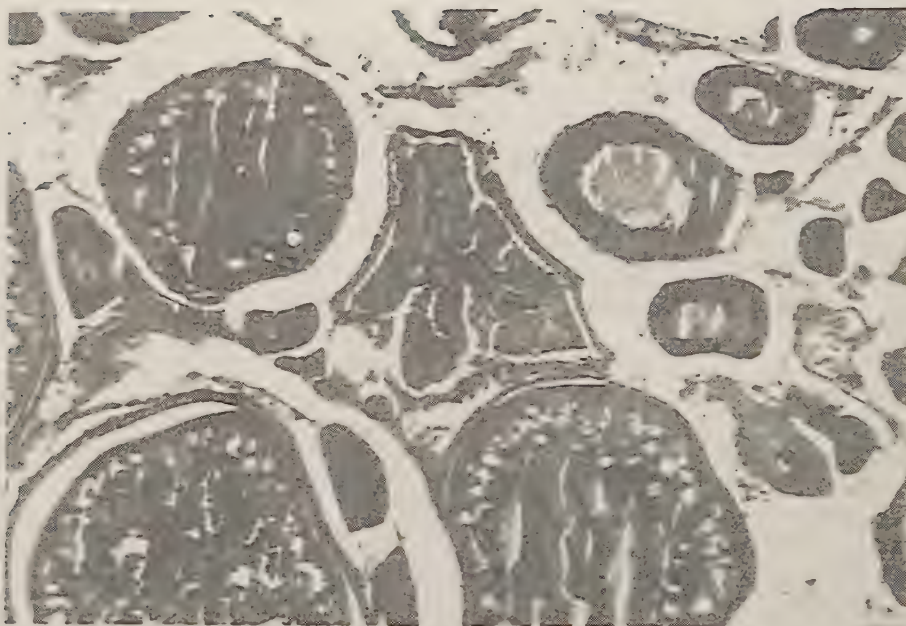


Fig. 1.—Postovulatory follicle, age Day-0. Elapsed time from spawning, about 0-5 h.

Fig. 1.—Folículo postovulatorio de 0 días de edad. Tiempo transcurrido desde la puesta de 0 a 5 horas.

and clearly distinguishable from the granulosa layer. The granulosa cells are polygonal and arranged in an orderly manner

along the lumen edge. The granulosa nuclei are evident, healthy, and linearly arranged (fig. 2).



Fig. 2.—Postovulatory follicle, age 19 h.

Fig. 2.—Folículo postovulatorio de 19 horas de edad.

Age 34-h postovulatory follicles

The follicular structure (fig. 3) tends to become more compact and shows a less irregular shape than the follicle previously described. The follicle layer presents fewer folds and loops. The thecal layer is still no-

derly manner, and present pycnotic nuclei. The lumen is very reduced. The number of postovulatory follicles per section appears to diminish. According to Hunter and Macewicz (1985), this reduction may be related to resorption or, alternatively, to the growth of the larger oocytes in the ovary.



Fig. 3.—Postovulatory follicle, age 34 h.

Fig. 3.—Folículo postovulatorio de 34 horas de edad.

ticeable and well differentiated from the granulosa layer, and contains groups of blood cells. The lumen is much reduced compared to the previous stage. The arrangement of granulosa cells is less orderly and, in a small number of them, pycnotic nuclei are present.

Age 61-h postovulatory follicles

The regressing follicle is more shrunken and has fewer folds than the 34-h follicle (fig. 4). Despite this, identification and classification is still possible. The theca layer is still present but, in some cases, it is indistinguishable from the granulosa layer. The granulosa cells are not arranged in an or-

Older than 61-h postovulatory follicles

The comparative analysis of postovulatory follicles from laboratory-spawned females and sea-caught females confirms that the degenerative processes of sardine follicles last beyond 61 hours after spawning. Thus, it was possible to differentiate another distinct stage of postovulatory follicle, with an age greater than 61 hours. This group can be characterized by a major reduction in their structure and occurrence. Generally, the follicle presents a triangular shape and the theca layer is totally indistinguishable from the granulosa layer. The lumen is very reduced or absent.

The persistence of postovulatory follicles in the sardine ovary longer than in the

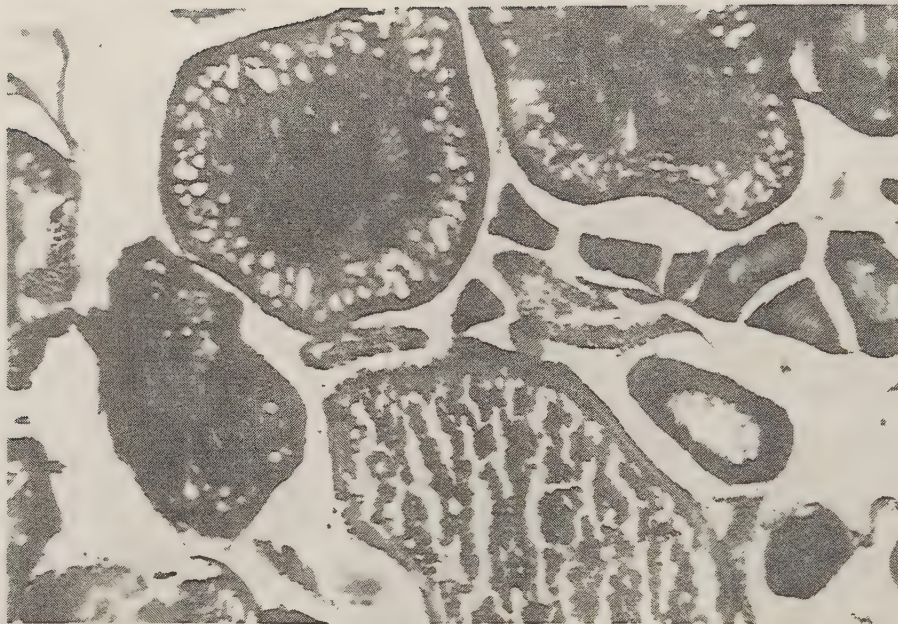


Fig. 4.—Postovulatory follicle, age 61 h.

Fig. 4.—Folículo postovulatorio de 61 horas de edad.

northern anchovy (*Engraulis mordax*) or the Peruvian anchovy (*Engraulis ringens*) but similar to duration in the Pacific sardine, may be related to differences in water temperature.

RESULTS AND DISCUSSION

The application of the Egg Production Method to the Atlantic Iberian sardine, *Sardina pilchardus*, required the estimation of the spawning fraction. Since spawning fraction is a daily estimate, the postovulatory follicle ages analyzed were grouped into four Day classes: Day-0 is ages from 0 to 6 hours after spawning; Day-1 is ages 18 to 30 hours; Day-2 is ages 42 to 54 hours; and Day-3 is ages older than 60 hours (sampling was not on a 24-hour basis; therefore, the "Days" reflect only ages actually encountered). It was decided that the estimation of the proportion of females spawning per day and per trawl should be based on the number of mature females whose postovulatory follicles were classified as Day-1 or Day-2,

i.e., $(\text{Day-1} + \text{Day-2})/2$ Pérez *et al.*, 1992). Day-3 follicles were not used since they presented ageing difficulties.

In Galicia (Spain), an oversampling of females with Day-0 follicles was observed, biasing the spawning fraction estimate (Pérez *et al.*, 1992). Notwithstanding, in Portugal the fraction of Day-0, Day-1 and Day-2 spawners did not reveal significant differences among them, indicating no bias in the Day-0 proportion (Cunha *et al.*, 1992). As a consequence, since Day-0 females can be overrepresented in the trawl stations, these females were not included in the spawning fraction estimate. The adjusted spawning fraction estimates by region along the Atlantic Iberian coast are summarized in table XI.

The low spawning fraction value for Galicia compared to the other regions was in agreement with sardine adult and egg distributions along the Atlantic Iberian coast. Along the Atlantic Iberian coast, the fraction of mature female sardine with less than 48-hour-old postovulatory follicles averaged 0.14 (standard deviation = 0.0122). This in-

indicated that the mean interval between each spawning was approximately 7 days.

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Table I.—Characteristics of the 12 collections of female sardine taken along the Galician coast during the DEPM Cruise (April-May 1988). (BT): bottom trawl.

Tabla I.—Características de las 12 colecciones de hembras de sardinas capturadas a lo largo de las costas de Galicia en la campaña del DEMP (abril-mayo 1988). (BT): arrastre demersal.

Collection number	Date (yyymmdd)	Time of day (hh.mm)	Average ovary-free weight (g)	Gear	Latitude N	Longitude W
1	880401	17.52	60.713	BT	42° 33.2'	08° 55.7'
2	880401	19.55	60.136	BT	42° 31.4'	08° 57.5'
3	880402	17.22	66.910	BT	42° 45.3'	09° 01.1'
6	880406	20.44	25.208	BT	42° 21.9'	08° 50.7'
8	880408	16.59	62.500	BT	43° 18.9'	08° 56.1'
12	880409	20.45	79.400	BT	43° 24.7'	08° 31.1'
13	880409	22.06	59.711	BT	43° 23.9'	08° 34.2'
14	880410	01.12	47.956	BT	43° 24.7'	08° 31.7'
19	880412	19.28	81.509	BT	43° 49.9'	07° 55.1'
20	880412	20.45	83.280	BT	43° 49.1'	07° 55.0'
21	880413	18.20	77.452	BT	43° 41.8'	07° 15.7'
22	880413	20.47	56.050	BT	43° 35.1'	07° 02.3'

Table II.—Characteristics of the 11 collections of female sardine taken along the western Cantabrian coast during the DEPM Cruise (April-May 1988). (BT): bottom trawl.

Tabla II.—Características de las 11 colecciones de hembras de sardinas capturadas a lo largo de las costas del Cantábrico occidental en la campaña del DEMP (abril-mayo 1988). (BT): arrastre demersal.

Collection number	Date (yyymmdd)	Time of day (hh.mm)	Average ovary-free weight (g)	Gear	Latitude N	Longitude W
24	880415	19.34	63.708	BT	43° 35.7'	06° 42.8'
25	880416	13.53	81.326	BT	43° 41.8'	06° 19.9'
26	880419	17.52	63.400	BT	43° 40.0'	06° 15.7'
28	880421	21.02	78.450	BT	43° 46.0'	05° 42.0'
30	880422	20.44	90.347	BT	43° 38.6'	05° 34.6'
31	880423	20.13	84.280	BT	43° 36.8'	05° 23.7'
32	880424	22.57	39.400	BT	43° 30.1'	04° 59.8'
33	880424	19.18	99.324	BT	43° 32.1'	04° 55.8'
35	880426	21.38	84.624	BT	43° 28.7'	04° 35.3'
36	880427	18.00	93.640	BT	43° 26.7'	04° 23.5'
37	880428	20.05	88.300	BT	43° 27.6'	04° 09.5'

Table III.—Characteristics of the 7 collections of female sardine taken along the eastern Cantabrian coast during the DEPM Cruise (April-May 1988). (BT): bottom trawl.

Tabla III.—Características de las 7 colecciones de hembras de sardinas capturadas a lo largo de las costas del Cantábrico oriental en la campaña del DEMP (abril-mayo 1988). (BT): arrastre demersal.

Collection number	Date (yyymmdd)	Time of day (hh.mm)	Average ovary-free weight (g)	Gear	Latitude N	Longitude W
38	880430	08.54	76.200	BT	43° 28.8'	03° 21.4'
39	880501	01.26	78.764	BT	43° 31.9'	03° 43.6'
40	880501	18.38	89.912	BT	43° 31.2'	03° 23.4'
41	880501	16.21	90.482	BT	43° 25.6'	03° 06.7'
42	880502	19.22	83.946	BT	43° 28.2'	02° 55.2'
43	880504	14.55	87.644	BT	43° 21.4'	02° 17.7'
44	880504	18.42	95.386	BT	43° 22.0'	02° 15.7'

Table IV.—Characteristics of the 7 collections of female sardine taken in the northern region of Portugal (north of Nazaré) during the DEPM Cruise (March 1988). (BT): bottom trawl and (PT): pelagic trawl.

Tabla IV.—Características de las 7 colecciones de hembras de sardinas capturadas a lo largo de la zona norte de Portugal (norte de Nazaré) en la campaña del DEMP (marzo 1988). (BT): arrastre demersal y (PT): arrastre pelágico.

Collection number	Date (yyymmdd)	Time of day (hh.mm)	Average ovary-free weight (g)	Gear	Latitude N	Longitude W
4	880301	21.30	40.24	BT	41° 35.2'	09° 01.1'
6	880303	03.32	17.55	BT	41° 13.6'	08° 56.2'
8	880303	23.37	32.42	BT	41° 09.0'	08° 56.3'
9	880306	10.16	46.58	BT	41° 02.6'	08° 45.5'
10	880306	13.42	48.47	PT	40° 57.3'	08° 54.0'
12	880307	16.30	19.94	PT	40° 21.1'	09° 03.5'
13	880307	20.24	26.14	BT	40° 35.1'	09° 02.1'

Table V.—Characteristics of the 2 collections of female sardine taken in the southern region of Portugal (south of Nazaré) during the DEPM Cruise (March 1988). (BT): bottom trawl and (PT): pelagic trawl.

Tabla V.—Características de las 2 colecciones de hembras de sardinas capturadas a lo largo de la zona sur de Portugal (sur de Nazaré) en la campaña del DEMP (marzo 1988). (BT): arrastre demersal y (PT): arrastre pelágico.

Collection number	Date (yyymmdd)	Time of day (hh.mm)	Average ovary-free weight (g)	Gear	Latitude N	Longitude W
1	880227	12.45	22.87	PT	38° 38.0'	09° 30.0'
18	880325	21.58	48.75	BT	38° 22.5'	08° 58.9'

Table VI.—Number of female sardine in different spawning and atresia states along the Galician coast during the DEPM Survey (April-May 1988). Legend: atresia states. (0): no alpha- α atresia of yolked oocytes. (1): alpha- α atresia in $< 50\%$ of yolked oocytes and (2): alpha- α atresia in $> 50\%$ of yolked oocytes.

Tabla VI.—Número de hembras de sardina en los diferentes estados de puesta y atresia obtenidas en aguas de las costas de Galicia durante la campaña del DEPM (abril-mayo 1988). Leyenda: estados de atresia. (0): no aparece atresia tipo α en los ovocitos vitelados, (1): atresia α aparece en menos del 50 % de los ovocitos vitelados y (2): atresia α aparece en más del 50 % de los ovocitos vitelados.

Collection number	Atresia state	Day-0	Day-1	Day-2	Nonspawning females	Tot. mature females	Tot. immature females
1	0	0	2	0	6	25	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	0	2	0	6	25	
2	0	16	1	2	6	25	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	16	1	2	6	25	
3	0	0	0	0	2	25	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	0	0	0	2	25	
6	0	0	0	0	3	3	0
	1	0	0	0	0	0	
	2	0	0	0	2	2	
	Total	0	0	0	5	5	
8	0	0	0	1	0	1	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	0	0	1	0	1	
12	0	0	0	0	0	0	0
	1	0	0	0	1	1	
	2	0	0	0	0	0	
	Total	0	0	0	1	1	
13	0	0	0	1	14	15	1
	1	0	0	0	1	1	
	2	0	0	0	2	2	
	Total	0	0	1	17	18	
14	0	0	0	2	10	12	1
	1	0	1	0	1	2	
	2	0	0	0	1	1	
	Total	0	1	2	12	15	

Table VI.—(Cont.)

Tabla VI.—(Cont.)

Collection number	Atresia state	Day-0	Day-1	Day-2	Nonspawning females	Tot. mature females	Tot. immature females
19	0	20	0	0	0	24	0
	1	1	0	0	0	1	
	2	0	0	0	0	0	
	Total	21	0	0	0	25	
20	0	24	1	0	0	25	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	24	1	0	0	25	
21	0	0	0	4	13	17	0
	1	0	0	0	3	3	
	2	0	0	1	4	5	
	Total	0	0	5	20	25	
22	0	1	0	2	10	13	0
	1	0	0	0	2	2	
	2	0	0	0	9	9	
	Total	1	0	2	21	24	

Table VII.—Number of female sardine in different spawning and atresia states along the western Cantabrian coast during the DEPM Survey (April-May 1988). Legend: atresia states. (0): no alpha- α atresia of yolked oocytes, (1): alpha- α atresia in < 50 % of yolked oocytes and (2): alpha- α atresia in > 50 % of yolked oocytes.

Tabla VII.—Número de hembras de sardina en los diferentes estados de puesta y atresia obtenidas en aguas de la costa oeste del Cantábrico durante la campaña del DEPM (abril-mayo 1988). Leyenda: estados de atresia. (0): no aparece atresia tipo α en los ovocitos vitelados, (1): atresia α aparece en menos del 50 % de los ovocitos vitelados y (2): atresia α aparece en más del 50 % de los ovocitos vitelados.

Collection number	Atresia state	Day-0	Day-1	Day-2	Nonspawning females	Tot. mature females	Tot. immature females
24	0	0	0	0	3	3	18
	1	0	0	0	4	4	
	2	0	0	0	0	0	
	Total	0	0	0	7	7	
25	0	0	0	1	6	23	1
	1	0	0	0	1	1	
	2	0	0	0	0	0	
	Total	0	0	1	7	24	

Table VII.—(Cont.)

Tabla VII.—(Cont.)

Collection number	Atresia state	Day-0	Day-1	Day-2	Nonspawning females	Tot. mature females	Tot. immature females
26	0	0	0	0	0	0	1
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	0	0	0	0	0	
28	0	0	3	0	11	14	1
	1	0	0	0	1	1	
	2	0	0	0	0	0	
	Total	0	3	0	12	15	
30	0	2	1	7	15	25	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	2	1	7	15	25	
31	0	0	2	6	13	21	0
	1	0	0	2	2	4	
	2	0	0	0	0	0	
	Total	0	2	8	15	25	
32	0	0	2	0	4	6	18
	1	0	0	0	1	1	
	2	2	0	0	0	0	
	Total	2	2	0	5	7	
33	0	0	2	7	12	23	0
	1	0	0	0	2	2	
	2	0	0	0	0	0	
	Total	0	2	7	14	25	
35	0	5	3	1	8	17	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	5	3	1	6	17	
36	0	0	1	3	15	20	0
	1	0	1	1	3	5	
	2	0	0	0	0	0	
	Total	0	2	4	18	25	
37	0	1	0	0	0	1	0
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	1	0	0	0	1	

Table VIII.—Number of female sardine in different spawning and atresia states along the eastern Cantabrian coast during the DEPM Survey (April-May 1988). Legend: atresia states. (0): no alpha- α atresia of yolked oocytes, (1): alpha- α atresia in < 50 % of yolked oocytes and (2): alpha- α atresia in > 50 % of yolked oocytes.

Tabla VIII.—Número de hembras de sardina en los diferentes estados de puesta y atresia obtenidas en aguas de la costa este del Cantábrico durante la campaña del DEMP (abril-mayo 1988). Leyenda: estados de atresia. (0): no aparece atresia tipo α en los ovocitos vitelados, (1): atresia α aparece en menos del 50 % de los ovocitos vitelados y (2): atresia α aparece en más del 50 % de los ovocitos vitelados.

Collection number	Atresia state	Day-0	Day-1	Day-2	Nonspawning females	Tot. mature females	Tot. immature females
38	0	0	0	0	1	1	0
	1	0	0	0	0	0	
	2	0	0	0	1	1	
Total		0	0	0	2	2	
39	0	5	5	4	4	18	0
	1	0	2	4	1	7	
	2	0	0	0	0	0	
Total		5	7	8	5	25	
40	0	0	5	3	12	22	0
	1	0	0	1	2	3	
	2	0	0	0	0	0	
Total		0	5	4	14	25	
41	0	0	7	2	7	24	0
	1	0	1	0	0	1	
	2	0	0	0	0	0	
Total		0	8	2	7	25	
42	0	0	5	6	11	23	0
	1	0	0	1	1	2	
	2	0	0	0	0	0	
Total		0	5	7	12	25	
43	0	0	3	2	2	7	0
	1	0	1	1	0	2	
	2	0	0	0	0	0	
Total		0	4	3	2	9	
44	0	0	3	4	14	21	0
	1	0	0	0	3	3	
	2	0	0	0	0	0	
Total		0	3	4	17	24	

Table IX.—Number of female sardine in different spawning and atresia states in the northern region of Portugal (north of Nazaré) during the DEPM Survey (March 1988). Legend: atresia states. (0): no alpha- α atresia of yolked oocytes, (1): alpha- α atresia in < 50 % of yolked oocytes and (2): alpha- α atresia in > 50 % of yolked oocytes.

Tabla IX.—Número de hembras de sardina en los diferentes estados de puesta y atresia obtenidas en aguas de Portugal (norte de Nazaré) durante la campaña del DEMP (marzo 1988). Leyenda: estados de atresia. (0): no aparece atresia tipo α en los ovocitos vitelados, (1): atresia α aparece en menos del 50 % de los ovocitos vitelados y (2): atresia α aparece en más del 50 % de los ovocitos vitelados.

Collection number	Atresia state	Day-0	Day-1	Day-2	Nonspawning females	Tot. mature females	Tot. immature females
4	0	3	11	6	9	33	0
	1	0	0	0	4	5	
	2	0	0	0	3	3	
	Total	3	11	6	16	41	
6	0	0	0	0	10	10	0
	1	0	0	0	2	2	
	2	0	0	0	1	1	
	Total	0	0	0	13	13	
8	0	2	1	1	19	21	1
	1	0	1	0	0	1	
	2	1	0	0	2	3	
	Total	3	2	1	21	25	
9	0	0	3	0	7	10	3
	1	0	0	0	0	0	
	2	0	0	0	0	0	
	Total	0	3	0	7	10	
10	0	0	1	5	16	22	1
	1	0	0	0	1	1	
	2	0	0	0	2	2	
	Total	0	1	5	19	25	
12	0	0	4	1	14	19	0
	1	0	1	0	4	5	
	2	1	0	0	1	2	
	Total	1	5	1	19	26	
13	0	0	3	5	10	22	1
	1	0	0	0	2	2	
	2	0	0	0	2	2	
	Total	0	3	5	14	26	

Table X.—Number of female sardine in different spawning and atresia states in the southern region of Portugal (south of Nazaré) during the DEPM Survey (March 1988). Legend: atresia states. (0): no alpha- α atresia of yolked oocytes, (1): alpha- α atresia in $< 50\%$ of yolked oocytes and (2): alpha- α atresia in $> 50\%$ of yolked oocytes.

Tabla X.—Número de hembras de sardina en los diferentes estados de puesta y atresia obtenidas en aguas de Portugal (sur de Nazaré) durante la campaña del DEMP (marzo 1988). Leyenda: estados de atresia. (0): no aparece atresia tipo α en los ovocitos vitelados, (1): atresia α aparece en menos del 50 % de los ovocitos vitelados y (2): atresia α aparece en más del 50 % de los ovocitos vitelados.

Collection number	Atresia state	Day-0	Day-1	Day-2	Nonspawning females	Tot. mature females	Tot. immature females
1	0	0	2	1	6	15	0
	1	1	0	1	1	7	
	2	0	0	0	1	1	
Total		1	2	2	8	23	
18	0	3	2	1	4	10	0
	1	1	1	1	1	4	
	2	0	0	0	0	0	
Total		4	3	2	5	14	

Table XI.—Adjusted estimates of the spawning fraction in the different regions of the Atlantic Iberian coast. Standard deviations in parentheses.

Tabla XI.—Estimaciones de la fracción de hembras reproductoras en las diferentes regiones de la costa atlántica de la península Ibérica. Desviación típica, entre paréntesis.

SPAIN			PORTUGAL		TOTAL
E Cant.	W Cant.	Galicia	North	South	
0.21 (0.0273)	0.13 (0.0143)	0.08 (0.0160)	0.13 (0.0357)	0.12 (0.0908)	0.14 (0.0122)

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PARKINSON'S PETREL DISTRIBUTION AND FORAGING ECOLOGY IN THE EASTERN PACIFIC: ASPECTS OF AN EXCLUSIVE FEEDING RELATIONSHIP WITH DOLPHINS¹

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Abstract. During 28 research vessel cruises in the eastern tropical Pacific Ocean from 1976 through 1990, Parkinson's Petrels (*Procellaria parkinsoni*) were observed near shore from southern Mexico (ca. 15°N) to northern Peru (ca. 5°S), and along a broad seaward extension that continued west of the Galápagos Islands to 110°W. Parkinson's Petrels regularly associated with dolphins: of the 618 petrels observed, 469 (76%) were associated with 10 species of dolphins, on 55 occasions, with 1 to 300 petrels present. They occurred mostly with two rare dolphin species: the melon-headed whale (*Peponocephala electra*) and the false killer whale (*Pseudorca crassidens*). This appeared to be a largely obligatory foraging relationship for Parkinson's Petrels. Associations with other dolphin species occurred primarily when those species also associated with melon-headed and false killer whales. Parkinson's Petrels avoided a common and widespread, multi-species feeding assemblage which consisted of a diverse, fast-moving group of seabirds, spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*), and tuna, all of which feed on live prey forced to the surface. The lumbering Parkinson's Petrels appeared ill-equipped to take such prey. In contrast, melon-headed and false killer whales apparently fed by dismembering large prey below the surface and so, provided feeding opportunities for a scavenging bird with diving capabilities. Among eastern tropical Pacific (ETP) seabirds, Parkinson's Petrels alone are adapted for recovering food scraps well below the surface. Parkinson's Petrels appear to be more dependent on marine mammals for foraging than any other species of seabird studied and feed diurnally more than was previously thought.

Key words: Parkinson's Petrel; *Procellaria parkinsoni*; feeding ecology; tropical seabirds; dolphin associations; scavenging.

INTRODUCTION

Seabirds are widely known to associate with sub-surface predators in order to feed on prey forced to the surface. Fish have been the predators most often identified, especially in the tropics where surface-feeding tunas are of major importance to foraging birds (Ashmole and Ashmole 1967, Erdman 1967, Colblentz 1985, Au and Pitman 1988, Hulsman 1988, Safina 1990). Similarly, marine mammals, especially cetaceans, have been shown to provide feeding opportunities for seabirds (Rumboll and Jehl 1977, Würsig and Würsig 1980, Evans 1982, Hoyt 1983, Blaber 1986, Enticott 1986, Martin 1986, Au and Pitman 1988, Pierotti 1988).

Evans (1982) reviewed seabird/cetacean interactions and concluded that seabirds' feeding with

cetaceans is largely opportunistic or incidental, but now there is evidence to the contrary. For example, Obst and Hunt (1990) found that gray whales (*Eschrichtius robustus*) provided a significant amount of food for seabirds foraging in the Bering Sea: up to 87% of the Red Phalaropes (*Phalaropus fulicarius*) and Black-legged Kittiwakes (*Rissa tridactyla*) they observed in the Chirikov Basin foraged in gray whales' mud plumes (see also Harrison 1979). Martin (1986) suggested that prey made available by Atlantic spotted dolphins (*Stenella frontalis*) was the most important source of food for Cory's Shearwaters (*Calonectris diomedea*) and Great Shearwaters (*Puffinus gravis*) foraging around the Azores Islands. Dusky dolphins (*Lagenorhynchus obscurus*) foraging off Argentina reportedly drove anchovies to the surface where thousands of seabirds sometimes gathered to feed for hours (Würsig and Würsig 1979, 1980). In the eastern tropical

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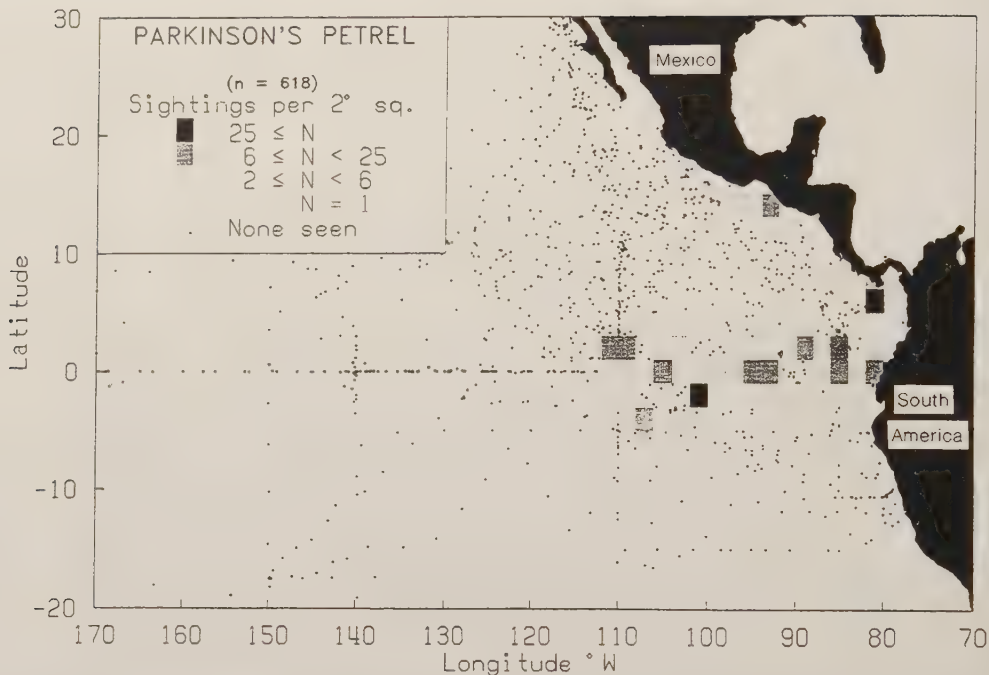


FIGURE 1. Sightings of Parkinson's Petrel in the eastern tropical Pacific, 1976–1990. Shaded areas represent total number of sightings per 2° square; dots represent noon vessel positions for days on which no petrels were observed.

Pacific (ETP), spotted dolphins (*Stenella attenuata*) and, to a lesser extent, spinner dolphins (*S. longirostris*) are part of a persistent and widespread feeding assemblage that includes large and diverse bird flocks and schools of surface-feeding tunas (Au and Pitman 1986, 1988). To this growing list we add a previously undescribed foraging relationship between two species of dolphins in the eastern Pacific and the little-known Parkinson's Petrel (*Procellaria parkinsoni*).

Parkinson's Petrel breeds on two islands off northern New Zealand where a remnant population of approximately 3,000–4,000 birds has been seriously threatened by introduced cats and other predators (Imber 1987). It nests during the austral summer (November–June), then migrates to the ETP to spend its non-breeding season (Loomis 1918, Murphy 1936, Jehl 1974, Imber 1976, Stiles and Smith 1977, Arnborn 1986, Ridgely and Gwynne 1989, this study). Because of this species' small population size and pelagic habits, little is known about its foraging ecology or distribution at sea. In this paper we present information on Parkinson's Petrel distribution,

feeding habits, and foraging associations in the ETP.

STUDY AREA

Our study area covered more than 10 million km² of open ocean between San Diego, California, and Lima, Peru, extending west roughly to the longitude of Hawaii, at approximately 155°W (Fig. 1). Two major surface currents are particularly relevant to this study: the South Equatorial Current, and the Equatorial Countercurrent (Wyrtki 1966). The South Equatorial Current is derived mainly from the cold Peru Current, which flows north along western South America, veers away from the northern coast of Peru at about latitude 5°S, and crosses the equator east of the Galápagos Islands before heading west between 1° and 3°N. To the north of this, the Equatorial Countercurrent, nominally between 4° and 10°N, flows east and is considerably warmer and less saline (i.e., more tropical). The boundary between these currents forms the Equatorial Front, an area of increased abundance of surface organisms (Wyrtki 1966, Pak and Zaneveld 1974).

METHODS

We recorded observations of Parkinson's Petrel during 28 research cruises from 1976 to 1990. Our survey effort of 1,687 days at sea was distributed fairly evenly throughout the study area (Fig. 1), during all months.

Research cruises were of two types: those designed to assess the status of dolphin stocks in the ETP and those designed to collect oceanographic information. The oceanographic cruises followed pre-determined tracks, with stops to collect data at pre-determined locations. The dolphin cruises also followed pre-determined tracks but diverted towards dolphin herds to identify species, estimate herd size, and count associated birds. On both cruise types, one or two observers scanned the ocean during most daylight hours when underway, using 20× or 25× mounted binoculars, and censused mammals using standard line-transect methods (see Holt and Sexton 1989 for details). We recorded *all* sightings of Parkinson's Petrels and seabird flocks (see below), regardless of distance from the ship, and noted any associated marine mammals and fishes. We also recorded the behavior of Parkinson's Petrel. One specimen was collected as it foraged among dolphins on 11 February 1977 at 5°52'S, 82°50'W (Los Angeles County Museum No. 85145).

To examine distribution, we plotted all Parkinson's Petrels seen per 2° latitude-longitude block regardless of whether seen while conducting survey or not (e.g., we included sightings at dawn and dusk or during bad weather). We did not plot sightings standardized for survey effort, but used the larger data set, because Parkinson's Petrel was rarely seen.

We analyzed Parkinson's Petrel associations with each cetacean species (some related taxa were lumped when there were no associations with them, e.g., *Balaenoptera* spp. and *Megaptera novaeangliae* were combined into the single category of "rorquals"). We also compared associations with distinct dolphin groups: (1) spotted and spinner dolphins, and (2) all the remaining dolphin species (see Au and Pitman 1986, 1988).

To characterize the relative abundance and species composition of the ETP cetacean community, we analyzed a detailed subset of data collected during four, four-month cruises from 1986 through 1989: 3,866 sightings of 23 ceta-

cean species sighted throughout the study area. Similarly, to describe seabird flocking associations with cetaceans and schooling fishes in the ETP, we used detailed flock data from the same 1986–1989 cruises: counts of 1,062 separate seabird flocks. When no Parkinson's Petrels were present, we defined a flock as five or more birds, but, to quantify all Parkinson's Petrel associations with other species, any group of two or more birds which contained Parkinson's Petrel was also defined as a flock.

To investigate foraging associations with subsurface predators, flocks were carefully scrutinized for associated marine mammals and schooling fishes (mainly tunas). Because dolphins must break the surface to breathe, few herds associated with birds were probably missed. Tunas, on the other hand, often stayed below the surface and were undoubtedly often overlooked; the number of times we observed tuna schools occurring with seabird flocks represents only a minimum value.

RESULTS

DISTRIBUTION AND OCCURRENCE IN THE ETP

We recorded 618 Parkinson's Petrels in the ETP (Fig. 1). They occurred near shore from at least southern Mexico (ca. 15°N) to northern Peru (ca. 5°S), and broadly seaward roughly on the equator or equatorial front, through the Galápagos Islands to at least 110°W.

We recorded Parkinson's Petrel in the ETP in all months except January; presumably some non-breeding birds can be found there year-round.

MARINE MAMMAL ASSOCIATIONS

Parkinson's Petrel regularly associated with herds of 10 species of delphinid cetaceans (some of the larger dolphins in the family *Delphinidae* are referred to by their common names as "whales"): 469 (75.9%) were associated with dolphins on 55 occasions (Table 1); the remaining 149 (24.1%) were single birds or flocks not associated with cetaceans. When occurring with dolphins, numbers ranged from 1 to 300 birds, with a mode of 1 (Fig. 2). Thirty Parkinson's Petrels (54.5% of sightings) were present as lone birds with dolphins, but single birds accounted for only 6.4% of the total number of associated petrels.

Parkinson's Petrel consistently associated with two species of dolphin: the melon-headed whale (*Peponocephala electra*) and the false killer whale

TABLE 1. Mean number ($\pm$ SD) of Parkinson's Petrels present per dolphin herd for herds with associated Parkinson's Petrels. Means are given for single-species herds and for mixed-species herds with and without false killer and melon-headed whales. (n) = number of herds with associated Parkinson's Petrels.

Dolphin species	Species composition of dolphin herds			
	Single-species herds	Mixed-species herds including False Killer Whale	Mixed-species herds including Melon-headed Whale	Mixed-species herds except those including False Killer Whale or Melon-headed Whale
Melon-headed whale <i>Peponocephala electra</i>	9.5 $\pm$ 13.8 (4)	—	—	—
False killer whale <i>Pseudorca crassidens</i>	4.0 $\pm$ 3.3 (9)	—	—	—
Killer whale <i>Orcinus orca</i>	1.5 $\pm$ 1.0 (4)	—	—	1.5 $\pm$ 1.0 (4)
Pilot whale <i>Globicephala macrorhynchus</i>	1.7 $\pm$ 0.6 (3)	14.0 (1)	—	1.9 $\pm$ 1.3 (10)
Common dolphin <i>Delphinus delphis</i>	1.5 $\pm$ 0.6 (6)	—	—	1.5 $\pm$ 0.6 (6)
Bottlenose dolphin <i>Tursiops truncatus</i>	1.7 $\pm$ 1.6 (6)	105.3 $\pm$ 168.6 (3)	10.0 (1)	1.7 $\pm$ 1.4 (16)
Risso's dolphin <i>Grampus griseus</i>	—	300.0 (1)	—	1.0 (1)
Spotted dolphin <i>Stenella attenuata</i>	1.0 $\pm$ 0.0 (2)	—	—	1.0 $\pm$ 0.0 (5)
Striped dolphin <i>Stenella coeruleoalba</i>	1.0 $\pm$ 0.0 (2)	—	—	1.0 $\pm$ 0.0 (2)
Spinner dolphin <i>Stenella longirostris</i>	—	—	—	1.0 $\pm$ 0.0 (3)

(*Pseudorca crassidens*) (Fig. 3). We analyzed the 1986–1989 marine mammal sightings data for associations with Parkinson's Petrel and rejected the null hypothesis that Parkinson's Petrel as-

sociated randomly with cetacean species in the ETP ($\chi^2 = 845.2$, $df = 16$, $P = 0.00$). Although melon-headed whales and false killer whales were rarely seen in the ETP (0.4% and 0.9% of the

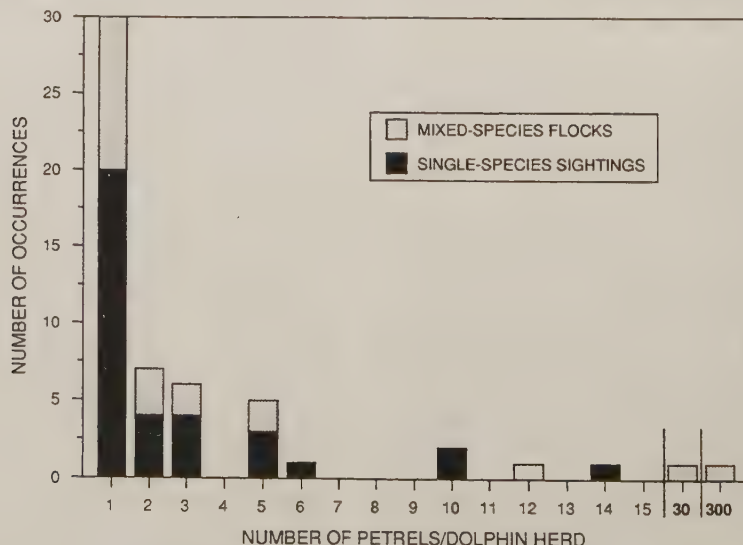


FIGURE 2. Frequency histogram of number of Parkinson's Petrels per herd for all dolphin herds with associated Parkinson's Petrels ($n = 55$ herds). Results are shown for single-species sightings (only Parkinson's Petrel present) and mixed-species flocks.

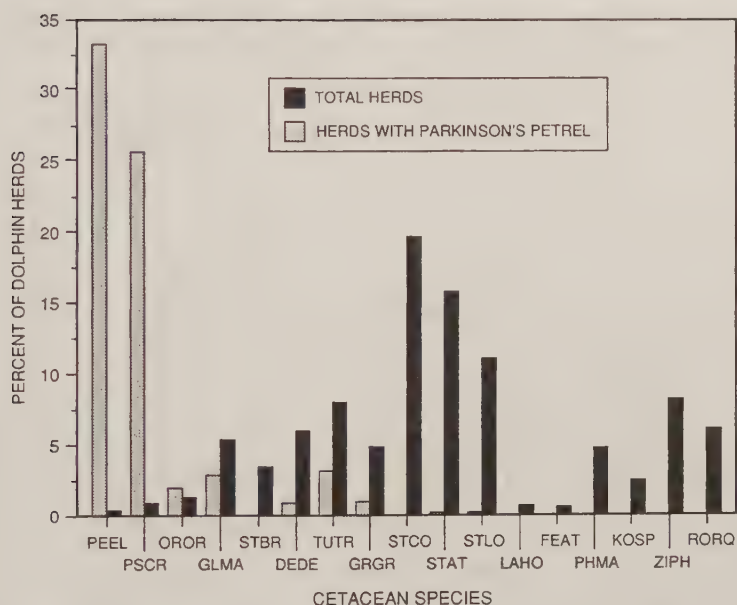


FIGURE 3. Relative sighting frequency of cetacean species (or species groups) recorded during 1986–1989 survey cruises and frequency of association with Parkinson's Petrels. (Example, 0.4% of all cetacean herds were PEEL, while 33.3% of all PEEL herds were with associated Parkinson's Petrels.) Species codes: PEEL—*Peponocephala electra*, melon-headed whale ($n = 15$ herds); PSCR—*Pseudorca crassidens*, false killer whale ($n = 35$ herds); OROR—*Orcinus orca*, killer whale ($n = 50$ herds); GLMA—*Globicephala macrorhynchus*, short-finned pilot whale ($n = 209$ herds); STBR—*Steno bredanensis*, rough-toothed dolphin ($n = 135$ herds); DEDE—*Delphinus delphis*, common dolphin ($n = 231$ herds); TUTR—*Tursiops truncatus*, bottlenose dolphin ($n = 309$ herds); GRGR—*Grampus griseus*, Risso's dolphin ($n = 190$ herds); STCO—*Stenella coeruleoalba*, striped dolphin ($n = 764$ herds); STAT—*S. attenuata*, spotted dolphin ($n = 613$ herds); STLO—*S. longirostris*, spinner dolphin ($n = 431$ herds); LAHO—*Lagenorhynchus hosei*, Fraser's dolphin ($n = 26$ herds); FEAT—*Feresa attenuata*, pygmy killer whale ($n = 25$ herds); PHMA—*Physeter macrocephalus*, sperm whale ($n = 184$ herds); KOSP—*Kogia* spp., dwarf and pygmy sperm whales ($n = 97$ herds); ZIPH—Ziphiidae, beaked whales ($n = 316$ herds); RORQ—*Megaptera novaeangliae* and *Balaenoptera* spp., rorquals ($n = 236$ herds).

total cetacean sightings, respectively), these two species had by far the highest incidences of association with Parkinson's Petrel: 33.3% of melon-headed whale herds and 25.7% of false killer whale herds were accompanied by petrels. In contrast, Parkinson's Petrel occurred with less than 3.5% of herds of each of the remaining cetacean species.

Melon-headed whales and false killer whales also had the highest average number of associated Parkinson's Petrels per attended single-species herd with 9.5 and 4.0 petrels, respectively (Table 1). The remaining species each averaged less than 2.0 petrels per single-species herd. The eight flocks containing the largest number of Parkinson's Petrels, including every aggregation of over five individuals, were with herds that had either melon-headed or false killer whales pres-

ent. The largest flock of Parkinson's Petrels, estimated at 300 birds, was associated with a mixed herd of false killer whales, bottlenose dolphins (*Tursiops truncatus*), and Risso's dolphins (*Grampus griseus*). This flock alone may have contained nearly 10% of the world population of this species!

We recorded high numbers of Parkinson's Petrels with other species of dolphins only when they occurred as mixed-species herds containing melon-headed or false killer whales (Table 1). Thus, the bottlenose dolphin, pilot whale (*Globicephala macrorhynchus*), and Risso's dolphin were important largely when they also associated with melon-headed and false killer whales. All other cetacean species were unimportant or completely ignored, although many were abundant in the study area (Fig. 3).

TABLE 2A. Mean number ($\pm$ SD) of Parkinson's Petrels in single-species sightings (i.e., Parkinson's Petrel was the only seabird present). 2B. Mean number of birds ($\pm$ SD) in mixed-species flocks containing Parkinson's Petrel. Means are given for three categories of dolphin associations.

Bird species	Dolphin association		
	No dolphins present	Dolphin species other than Spotted or Spinner	Only Spotted or Spinner present
A: Single-species sightings	(n = 112)	(n = 34)	(n = 1)
Parkinson's Petrel <i>Procellaria parkinsoni</i>	1.0 $\pm$ 0.1	2.7 $\pm$ 3.1	1.0
B: Mixed-species flocks	(n = 4)	(n = 15)	(n = 4)
Parkinson's Petrel <i>P. parkinsoni</i>	1.0 $\pm$ 0.0	24.6 $\pm$ 76.6	1.0 $\pm$ 0.0
Galápagos Storm-Petrel <i>Oceanodroma tethys</i>	13.3 $\pm$ 18.8	36.4 $\pm$ 64.0	—
Unidentified storm-petrel <i>Oceanodroma</i> sp.	—	9.8 $\pm$ 9.5	—
Unidentified frigatebird <i>Fregata</i> sp.	—	2.7 $\pm$ 1.5	—
Tahiti Petrel <i>Pterodroma rostrata</i>	1.2 $\pm$ 0.0	—	—
Markham's Storm-Petrel <i>O. markhami</i>	1.0 $\pm$ 0.0	0.1 $\pm$ 0.0	—
Wedge-tailed Shearwater <i>Puffinus pacificus</i>	—	0.1 $\pm$ 0.0	142.0 $\pm$ 127.4
Juan Fernandez Petrel <i>Pt. externa</i>	—	—	47.5 $\pm$ 38.9
Masked Booby <i>Sula dactylatra</i>	—	0.1 $\pm$ 0.0	18.8 $\pm$ 14.1
Red-footed Booby <i>S. sula</i>	—	—	8.7 $\pm$ 9.9
Pink-footed Shearwater <i>P. creatopus</i>	—	0.1 $\pm$ 0.0	7.5 $\pm$ 5.2
Arctic Tern <i>Sterna paradisaea</i>	—	2.7 $\pm$ 2.1	4.0 $\pm$ 4.2
Pomarine Jaeger <i>Stercorarius pomarinus</i>	—	—	4.0 $\pm$ 1.4
Unidentified shearwater <i>Puffinus</i> sp.	—	—	—
Christmas Island Shearwater <i>P. nativitatus</i>	—	0.1 $\pm$ 0.0	—
Dark-rumped Petrel <i>Pt. phaeopygia</i>	0.8 $\pm$ 0.0	—	0.2 $\pm$ 0.0
White-bellied Storm-Petrel <i>Fregetta grallaria</i>	—	0.2 $\pm$ 0.0	—
Unidentified booby <i>Sula</i> sp.	—	0.1 $\pm$ 0.0	—
Magnificent Frigatebird <i>F. magnificens</i>	—	0.1 $\pm$ 0.0	—
Unidentified jaeger <i>Stercorarius</i> sp.	—	0.3 $\pm$ 0.0	—
Parasitic/Long-tailed Jaeger	—	—	0.2 $\pm$ 0.0
<i>S. parasiticus/longirostris</i>	—	—	0.2 $\pm$ 0.0

MARINE BIRD ASSOCIATIONS

We observed Parkinson's Petrel associated with a total of 15 species of marine birds on 23 separate occasions. Sightings consisted of both single-species (only Parkinson's Petrel present; Table 2A) and mixed-species flocks (Table 2B), with or without dolphins present.

Flocks without dolphins. We saw Parkinson's Petrels in mixed-species flocks without dolphins on only four occasions and in each case only one petrel was present (Table 2B). In each of the four cases the total flock size was small ($\bar{x}$ = 13.0 birds of other species; SD = 14.8), with few species ($\bar{x}$ = 1.5 other species, SD = 0.6), and all the birds appeared to be scavenging (i.e., we saw something floating on the surface that the birds were picking at). Galápagos Storm-Petrels (*Oceanodroma tethys*) constituted 77% of the individuals of the associated other species.

When not associated with dolphins or other species of birds, of Parkinson's Petrels not ini-

tially sighted as ship followers, 110 (98%) were single birds and the remaining two (2%) were a lone pair.

Flocks with dolphins. Most flocks containing Parkinson's Petrels occurred with dolphin herds, including 15 of 16 (94%) single-species flocks and 19 of 23 (83%) mixed-species flocks. Parkinson's Petrels were also more numerous in flocks associated with dolphins: the mean number of petrels per sighting with dolphins other than spotted/spinner herds, was significantly higher than without dolphins, for both single- and mixed-species flocks (Mann-Whitney U = 1,066.0, P = 0.00; Mann-Whitney U = 10.0, P = 0.03, respectively; Table 2A, B).

Parkinson's Petrel was often the only bird species present when it occurred with dolphins (Fig. 2). Of the 55 times we recorded it with dolphins, it was the only species present on 35 occasions (64%). The number of Parkinson's Petrels present in single-species flocks with dolphins ranged from 1 to 14 with a mode of 1. When Parkinson's

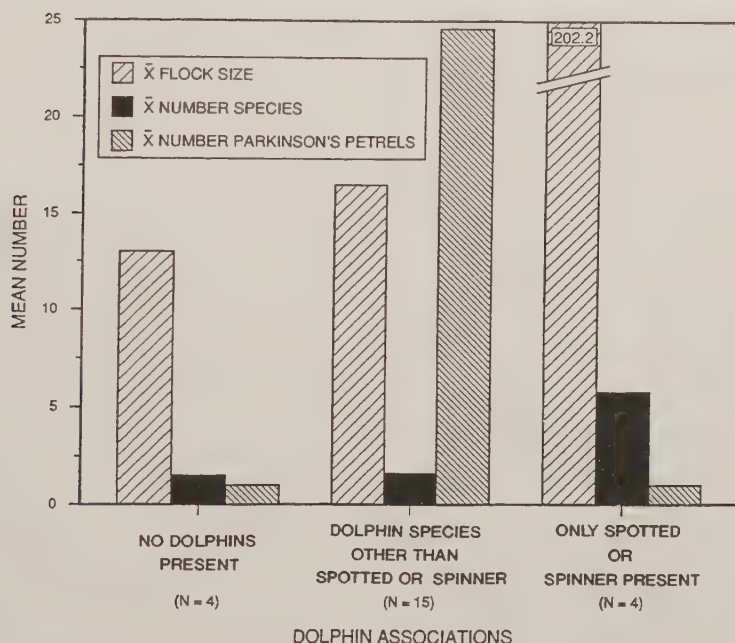


FIGURE 4. Associations between seabird flocks containing Parkinson's Petrels and dolphin herds. Shown are mean flock size (less Parkinson's Petrel), mean number of bird species (less Parkinson's Petrel), and mean number of Parkinson's Petrels for each of three categories of dolphin associations: a) flocks not associated with dolphin herds, b) flocks associated with herds other than spotted/spinner dolphins, and c) flocks associated with spotted/spinner herds only.

Petrels did occur in mixed-species flocks, there were usually very few individuals of other bird species present. For example, on 6 of the 19 occasions when Parkinson's Petrel occurred in mixed-species flocks with dolphins, only one bird of another species was present.

Mixed-species flocks containing Parkinson's Petrels and associated with spotted and spinner dolphins (Table 2B, Fig. 4) were large ($\bar{x} = 202.2$ birds of other species, $SD = 139.6$), diverse ($\bar{x} = 6.0$ other species, $SD = 0.8$), and had only single Parkinson's Petrels. These were dominated by a different group of bird species: the Wedge-tailed Shearwater (*Puffinus pacificus*), Juan Fernandez Petrel (*Pterodroma externa*), and Masked and Red-footed boobies (*Sula dactylatra* and *S. sula*). Flocks with Parkinson's Petrels but associated with dolphin species other than spotted and spinner dolphins, were relatively small ($\bar{x} = 17.5$ birds of other species, $SD = 37.8$), had few species ($\bar{x} = 1.7$ other species, $SD = 0.8$), but typically had a large number of Parkinson's Petrels ($\bar{x} = 24.6$, $SD = 76.6$) and storm-petrels (see the first group of six taxa in Table 2B). Of the 255 birds of nine

species that comprised this flock category, 182 (71%) were Galápagos Storm-Petrels (*Oceanodroma tethys*), the only seabird that regularly occurred with Parkinson's Petrel. We recorded 1,062 seabird flocks during 1986–1989; of these 217 (20.4%) were associated with spotted and spinner dolphins but only a single Parkinson's Petrel was present.

SCHOOL FISH ASSOCIATIONS

Unlike many other species of ETP seabirds, Parkinson's Petrel almost never foraged in association with surface-feeding tunas: only four (0.6%) individuals, all singles, were so observed, and spotted or spotted and spinner dolphins were also present. We never observed tunas present when Parkinson's Petrel was with any other species of dolphin.

Among 1,062 bird flocks recorded in 1986–1989, a minimum of 192 (18.1%) were associated with tuna, and, of these, 125 (65.1%) were also associated with spotted and/or spinner dolphins, but we recorded only one Parkinson's Petrel with them.

FORAGING BEHAVIOR

We observed three types of potential foraging by Parkinson's Petrel in the ETP. In increasing order of observed importance they were: scavenging dead prey (0.5% of the total individuals observed), following ships to pick through garbage and offal (8.0%), and associating with dolphin herds (75.9%). The remaining individuals (15.6%) were unassociated traveling birds.

Scavenged natural prey appeared to be primarily floating dead squid and was the least important food source we identified, as only single birds fed on it and then only rarely.

Ship-following may have been a more dependable food source for Parkinson's Petrel. A total of 49 birds joined our vessel, with a maximum of nine at any one time. This represents 8.0% of the total number of petrels seen and 38.0% of the birds not associated with other birds or dolphins (only unassociated birds came over to our vessel). We observed ship-followers picking through garbage and scavenging bait and discarded fishing offal. Ship-following was especially common near shore: we had up to five petrels at a time in our wake off the Azuero Peninsula, Panama, where Panama Canal traffic was always heavy.

Associating with dolphins was the most common type of foraging we observed. On 11 February 1977 at 11:30 hr, Pitman observed a lone Parkinson's Petrel associated with a herd of bottlenose dolphins. Each time the dolphins surfaced from a dive, the petrel flew over to them, landed with its wings held high and partially extended, and put its head underwater. This was the normal searching mode we observed when Parkinson's Petrels associated with dolphins, except that on other occasions we often saw birds dive from the surface. Pitman collected this bird subsequent to these observations. Its stomach contained the remains of a recently ingested squid, identified to family *Octopoteuthidae*, probably *Octopoteuthis* sp. by D. Au (pers. comm., SWFSC, La Jolla, CA).

Parkinson's Petrel is a capable diver. On 15 May 1986, a pair of petrels associated with a herd of pilot whales came close to our stopped vessel and Pitman attracted them with pieces of squid. The squid sank but the birds were able to dive from the surface and stay submerged for up to 20 seconds before surfacing with the bait. It was difficult to judge how deep they went, but

they almost disappeared in clear blue water and Pitman estimated they were going down at least 10 m.

DISCUSSION

DISTRIBUTION

Along the coast of the Americas, Parkinson's Petrels appeared to concentrate adjacent to areas of upwelling associated with the Gulf of Tehuantepec (surrounded by the northernmost cluster of sightings in Fig. 1; Blackburn 1962) and Gulf of Panama (Forsberg 1963). The southernmost limit of distribution along the mainland coast was at about 5°S where the cooler water of the Peru current veers west from the coast of Peru at the equatorial front. This front continues west, out beyond Galápagos, and may have formed the physical axis and biological basis for the westward extension of the range of Parkinson's Petrel in the ETP.

The location of the equatorial front is somewhat variable and fluctuates according to seasonal changes in the intensity of the Peru Current (Wyrtki 1966), and in response to longer term oceanographic variability. The only occurrence known to us of Parkinson's Petrel south of latitude 6°S in the ETP was a specimen found on the beach near Lurin, Peru (12°16'S), in February 1983 (identified by G. Watson from a photograph, specimen not saved; M. Plenge, in litt.). This was when the pronounced 1982-1983 El Niño was transporting warm tropical water and associated organisms farther south than normal along the coast of South America (Barber and Chavez 1983, Velez et al. 1984), including, apparently, Parkinson's Petrel.

Why should Parkinson's Petrel restrict its non-breeding range to the ETP when all of the dolphin species it associates with are pan-tropical? The ETP is characterized by having a permanent shallow thermocline which is related to its unusually high productivity (Wyrtki 1966). The ETP is also the only place in the world where large yellowfin tuna (*Thunnus albacares*) and spotted and spinner dolphins are known to regularly occur together and to feed at the surface (Au and Perryman 1985). It has been suggested that this shallow thermocline may constrain, or allow, large tunas to forage at or near the surface in the highly productive mixed layer (Au and Perryman 1985). It is possible that this feature also allows other predators, such as melon-headed and false killer

whales, to feed closer to the surface—close enough for the relatively shallow-diving Parkinson's Petrel to successfully interact with them.

FORAGING ECOLOGY

Jackson's (1988) suggestion that "a natural tendency to exploit the feeding activity of whales may account for the propensity of White-chinned Petrels [*Procellaria aequinoctialis*] to scavenge behind fishing vessels" applies equally well to Parkinson's Petrel, and may account for its ship-following and trash-picking habits in general. But our observations suggest that associating with dolphins is the main food source for Parkinson's Petrel in the ETP, where we think they feed mainly by scavenging.

The seabird/dolphin/tuna assemblage that Parkinson's Petrel ignored involves seabirds taking live prey forced to the surface by tunas and dolphins (Au and Pitman 1986, 1988). Spotted and spinner dolphins and tuna are swift predators and in most of the hundreds of feeding bouts we have observed, fleeing prey were conspicuous, often leaping or flying out of the water to avoid predation. The prey, often flying fish and flying squid, were typically small: birds caught them live and swallowed them whole. Not surprisingly, seabirds that worked these aggregations were highly mobile; they tended to be plunge divers (boobies) or high-speed aerialists (terns, frigatebirds, shearwaters, *Pterodroma* petrels), and most were adept at aerial feeding (Gould 1971, Pitman, pers. observ.). In these situations, dolphins and tunas acted as "beaters" for foraging birds as described by Diamond (1981).

In contrast, we think that Parkinson's Petrel feeds mainly by diving under the surface and retrieving sinking scraps of large prey dismembered by larger, generally slower-swimming species of dolphins feeding below the surface. We base our conclusion on several pieces of evidence. First, we have observed the four dolphin species that Parkinson's Petrel associated with most often (false killer whale, melon-headed whale, pilot whale and bottlenose dolphin) on many occasions in the ETP and we have never seen prey visible at the surface when these animals appeared to be feeding. Second, of the many times we observed Parkinson's Petrels in the company of these dolphins, we never saw the birds feeding at the surface, although we saw them dive below the surface on many occasions. Finally, the diving capability that we observed

and the heavy, hooked bill of Parkinson's Petrel makes it well suited for scavenging prey below the surface. Also, it seems unlikely that Parkinson's Petrel would have the speed underwater to catch live prey in relatively clear tropical water.

There are several published accounts of dolphins making food available for scavenging seabirds. Martin (1986) reported that Cory's Shearwaters and Great Shearwaters feeding among herds of Atlantic spotted dolphins took mainly scraps or wounded fish, and only occasionally took whole, live prey. Seabirds have often been seen feeding on offal left by killer whales (e.g., Lillie 1955, Jacobsen 1986, Rice and Saayman 1987, Reeves and Mitchell 1988, Wenzel and Sears 1988), and on two occasions in the ETP we have seen birds collect around dolphin entails floating at the surface after killer whale attacks. Seabirds are also reported to feed on squid remains vomited by sperm whales (*Physeter macrocephalus*) (Clarke et al. 1981).

An additional way that dolphins might make prey available to scavenging seabirds comes from Clarke et al. (1988). While investigating the feeding habits of sperm whales captured off Peru and Chile, they noticed that there were many more squid bodies than squid heads in the whales' stomachs. From this they hypothesized that captured squid often cling to the outside of the whale's head with their tentacles and when the whale swallows the bodies the decapitated heads later drop off and are lost. Although the heads probably sink when they fall off (Clarke et al. 1979), a diving bird such as Parkinson's Petrel might have a chance at retrieving these parts. Currently, the only direct evidence we have that this kind of feeding may happen comes from Roberson (pers. comm.), who observed a White-chinned Petrel diving among pilot whales off northern Peru and reported that "one appeared to actually strike the head of one surfacing pilot whale."

Although there is little specific information available on the feeding habits of the false killer whale, it is known to take large prey which could provide feeding opportunities for scavengers. Perryman and Foster (1980) described instances of false killer whales attacking dolphins during tuna purse seine fishing operations in the ETP and Hoyt (1983) reported an attack on a humpback whale calf. Watson (1981) observed several members of a group of feeding false killer whales each carrying a single large fish crosswise in its mouth. He also described captive false killer

whales shaking large fish until the head and entrails fell free, then peeling off the skin before swallowing the fillet.

Almost nothing is known about the food or feeding habits of the melon-headed whale. Mead et al. (cited in Perryman et al., in press) examined the stomach contents of a herd of melon-headed whales that stranded on the Pacific coast of Costa Rica. They found large numbers of ommastrephid squid beaks (primarily *Dosidicus gigas*), and, based on the squid beak measurements, they postulated that melon-headed whales were taking larger squid than were spotted and spinner dolphins in the same area.

Evidence suggests that all *Procellaria* petrels feed as scavengers, at times in association with dolphins. The Grey Petrel (*P. cinerea*) is a proficient diver (Brothers 1991:259) and has been observed foraging with cetaceans (Rumboll and Jehl 1977, Blaber 1986). Little is known about the foraging habits of the Westland Petrel (*P. westlandica*), except that it readily takes offal from fishing boats (Bartle 1985). The White-chinned Petrel readily takes fishing vessel offal when it is available (Jackson 1988); it is able to "dive well below the surface" (Murphy 1936:647), and Enticott (1986) found that it was more commonly associated with cetaceans than any other species of southern seabird in his study. Ridoux (1987) reported White-chinned Petrels followed killer whales even when the whales were not feeding, apparently in anticipation of feeding opportunities and we have seen Parkinson's Petrels in the ETP following false killer whales, possibly for the same reason. Our results suggest that Parkinson's Petrels, at least while in the ETP, has expanded this foraging relationship and become more dependent on cetaceans than has been suggested for any other seabird species to date.

A final point concerns the extent to which Parkinson's Petrel feeds at night. Imber (1976) studied Parkinson's Petrel diet in New Zealand during the breeding season and suggested that it is predominantly a nocturnal feeder because its diet consists largely of prey items, mainly squid, that he believed are present at the surface only at night because they might migrate to deeper water during the day. He also noted that bioluminescent forms predominate in the diet, which he argued was further evidence for nocturnal feeding. Our observations indicate that Parkinson's Petrels, at least while in the ETP, are more diurnal in their foraging than Imber (1976) has

suggested. A habit of foraging with deep-diving dolphins during the daytime might also explain a diet of prey not normally expected to be available to a diurnal seabird. Although our observations do not preclude nocturnal feeding, they do indicate a need for additional study.

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Abstract.—Research and commercial trapping data show variation in recruitment to the fishery for spiny lobster *Panulirus marginatus* at Maro Reef, relative to Necker Island which is 670 km to the south-east. Recruitment to the fishery at Maro Reef is shown to be highly correlated with the difference in sea level 4 years earlier between French Frigate Shoals and Midway Islands. Geosat altimeter data indicate that the relative sea level between French Frigate Shoals and Midway is an indicator of the strength of the Subtropical Counter Current. Mechanisms linking the Subtropical Counter Current with larval advection and survival are discussed. The sea level index provides a forecast of recruitment 4 years later to the fishery at Maro Reef.

Variability in spiny lobster *Panulirus marginatus* recruitment and sea level in the Northwestern Hawaiian Islands*

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Significant correlations between commercial landings or recruitment estimates and one or more environmental indices are commonly reported in the fisheries literature, but few have served as accurate predictors of future population levels (Drinkwater and Myers 1987). However, such correlations can lead to the formulation or support of hypotheses regarding the factors responsible for population changes. For example, an inverse correlation between the survival of Pacific mackerel *Scomber japonicus* to age 1 and the strength of the California Current, and the lack of correlation between survival and plankton biomass, have been offered as evidence that advection, rather than starvation, controlled survival of the planktonic stages of this species (Sinclair et al. 1985).

Correlative studies on lobsters suggest that population size results from changes in survival and advection at the larval stage, but in at least one

instance, density-dependent mechanisms after postsettlement may dampen this variation (Pollock 1986). Fluctuations in sea-surface temperature appear to result in changes in larval survival and catches 6 years later for the clawed lobster *Homarus americanus* in Maine (Fogarty 1988). Variation in the strength of the Leeuwin Current, which may be linked to El Niño Southern Oscillation (ENSO) events, is suggested as a cause of variation in the number of larvae returned to the coast and subsequent recruitment to the fishery for the western rock lobster *Panulirus argus* (Pearce and Phillips 1988). Changes in recruitment levels of the California spiny lobster *P. interruptus* to the northern portion of its habitat may be episodic, influenced by large-scale, interannual El Niño events (Pringle 1986). Variation in postlarval recruitment in the South African rock lobster *Jasus lalandii* is thought to arise from changes in the paths and velocities of extensive offshore currents, which eventually return larvae to the coast. However, density-dependent phenomena influ-

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encing juvenile and adult stages may substantially dampen this variation and produce fairly stable recruitment to the fishery (Pollock 1986).

In the Northwestern Hawaiian Islands (NWHI), a substantial drop in catches and catch-per-unit-effort (CPUE) of spiny lobster *P. marginatus* Quoy and Gaimard 1825 was recently documented (Polovina 1991). This study examines whether these declines in catches and CPUE are due to overfishing or to oceanographic factors which impact spiny lobster population dynamics.

NWHI lobster fishery

The NWHI region is an isolated range of islands, islets,

banks, and reefs that extend 2775 km northwest from Nihoa Island to Kure Atoll (Fig. 1). In 1977 after research cruises documented a substantial lobster population in the NWHI, a commercial trap fishery was initiated. The fishery targeted two species: the endemic spiny lobster *P. marginatus* and the slipper lobster *Scyllarides squammosus* Mike-Edwards 1837. A fishery management plan implemented in 1983 mandated that vessels submit logbooks recording daily catch and number of traps set (effort); the plan also established a minimum harvest size for spiny lobster and prohibited the harvest of egg-bearing females. Subsequent amendments to this plan added a minimum legal size for slipper lobster and required that traps have escape vents. In 1990, low catches and CPUE prompted a 6-month closure of the fishery (May–November 1991).

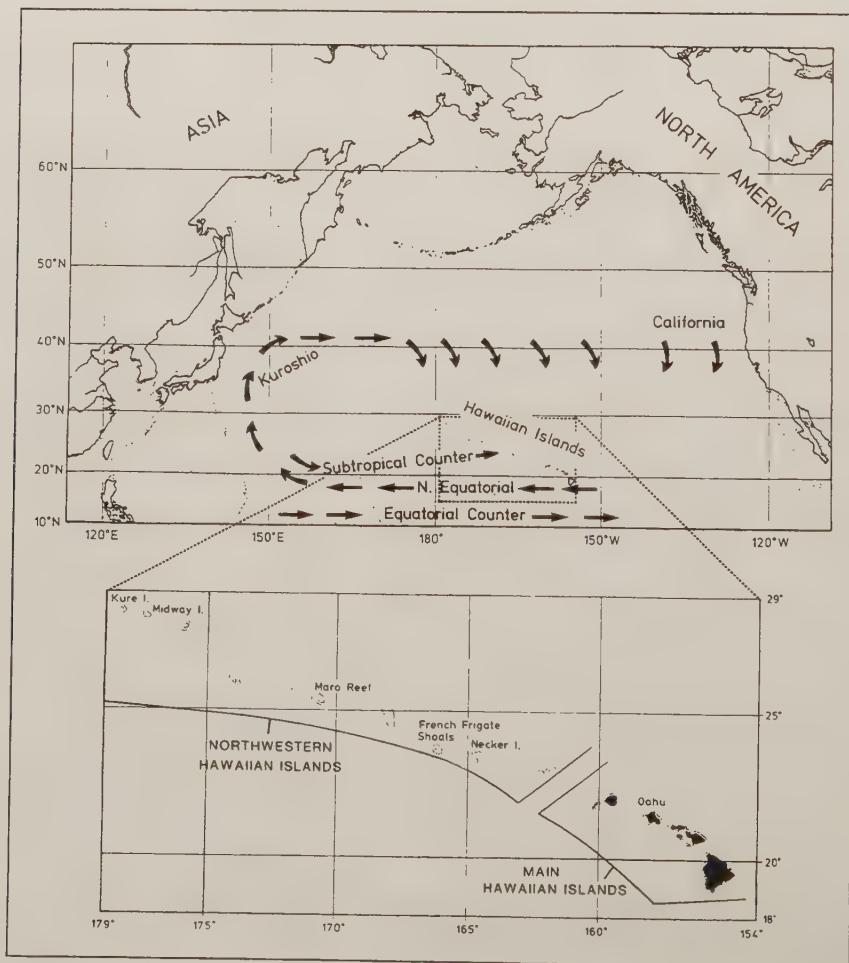


Figure 1

Pacific Ocean and major currents with an inset of the Hawaiian Archipelago, including the Northwestern Hawaiian Is.

Since 1983, the lobster fleet has been composed of 9–14 vessels (20–30 m long), each averaging 3 trips per year. The vessels set about 800 traps per day and remain at sea almost 2 months per trip. Landings in recent years have averaged almost 1 million lobsters, valued at about US\$6 million ex-vessel. Because of heavy fishing since 1986, the population has been fished down to the point that 3-year-old recruits comprised most of the fishery catches (Polovina 1991). Since 1988, about 80% of landings have been spiny lobster (Table 1). Two banks—Necker I. at the southeast end of the NWHI, and Maro Reef which is 670 km northwest of Necker I.—account for over 60% of the fishery's catches. There is no recreational lobster fishery in the NWHI.

Spiny lobster spawn over a broad spring, summer, and fall period. After hatching, the eggs are planktonic; the planktonic period for the larvae is estimated at 12 months based on spawning season and larval tow data (NMFS Honolulu Lab., unpubl. data). Further, the larval tow data suggest that mid- to late-stage spiny lobster larvae are close to the surface at night and move down to ~100 m during the day (Polovina, pers. observ.). Based on growth curves estimated from both tagging (MacDonald 1984) and length-based methods (Polovina and Moffitt 1989), spiny lobster reach the minimum legal size (which is slightly larger than the size at onset of sexual maturity) approximately 3 years after they settle onto benthic habitat. After settlement, the lobster probably do not move between banks since interbank depths exceed 1000 m.

Regional oceanography

The Hawaiian Archipelago lies within the subtropical gyre formed by the Kuroshio Current to the west and the north, the California Current to the east, and the North Equatorial Current to the south (Fig. 1). The speed of the gyre in the vicinity of the archipelago is slow (<5 cm/s; Roden 1991). An eastward-flowing current within the subtropical gyre, named the Subtropical Counter Current (SCC), was predicted by Yoshida and Kidokoro (1967) and subsequently confirmed by Robinson (1969) and Uda and Hasunuma (1969) (Fig. 1). More recent work has shown that, in at least the western portion, the interior of the subtropical gyre is composed

Table 1
Annual landings of spiny (*Panulirus marginatus*) and slipper (*Scyllarides squammosus*) lobsters, trapping effort, and percentage of spiny lobster in the landings, 1983–90.¹

Year	Lobster landings (10 ³)			Trap hauls (10 ³)	CPUE	% spiny lobster
	Spiny	Slipper	Total			
1983 ²	158	18	176	64	2.75	90
1984	677	207	884	371	2.38	78
1985	1022	900	1922	1041	1.83	53
1986	843	851	1694	1293	1.31	50
1987	393	352	745	806	0.92	53
1988	888	174	1062	840	1.26	84
1989	944	222	1166	1069	1.09	81
1990	591	187	778	1182	0.66	76

¹Data were provided to the NMFS Honolulu Lab., as required by the Crustacean Fishery Management Plan of the W. Pac. Reg. Fish. Manage. Council, Honolulu.

²April–December 1983.

of a quasi-stationary banded structure of easterly- and westerly-flowing currents (White and Hasunuma 1982). The SCC consists of two bands of eastward flow at 23° and 28°N, with mean annual speeds of 8 and 6 cm/s, respectively (White and Hasunuma 1982).

In addition to these large-scale features, the meso-scale oceanography around the Hawaiian Archipelago is a complex system of fronts and eddies resulting from both interactions between alternating east and west currents and interactions between current and the topography of the archipelago.

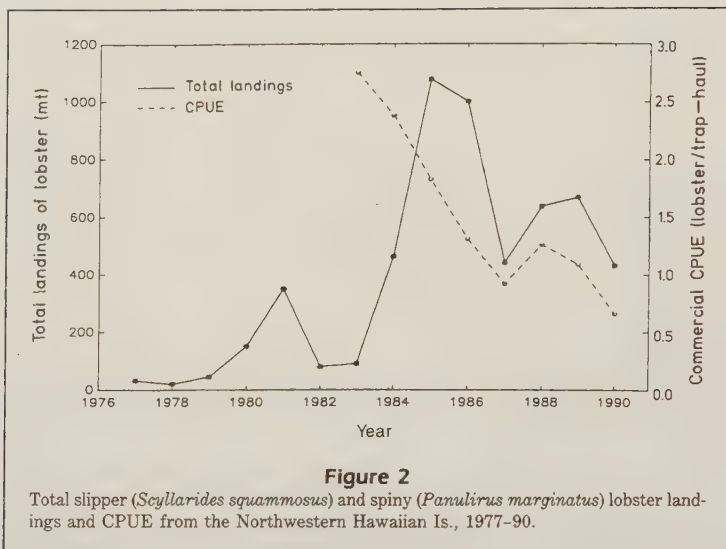
Data and analysis

Research data

Standardized trapping surveys, using the same traps set at the same sites, were conducted at Necker I. and Maro Reef during June and July of 1986–88 and 1990. The size-frequency data were converted to age-frequency data with a von Bertalanffy growth curve (MacDonald 1984). The age-frequency distribution was standardized for the number of traps deployed to estimate the relative age-frequency distribution of the population.

Fishery data

Although detailed catch and effort data were not available until after the logbook regulations were established in 1988, catch and effort were generally light and were concentrated around Necker I. from the inception of the fishery until 1984 (Fig. 2). The combined CPUE for slipper and spiny lobsters in 1983–90 generally declined from 2.8 to ~0.7 lobster per trap-



haul (Fig. 2), based on catch and effort data reported in the logbooks. Catch data in the logbooks are checked against landings by enforcement agents, so misreporting is not a problem. Common assessment approaches, such as length-based cohort analysis, are not applicable to this fishery, given the relatively short time-series of catch and effort data, the difficulty in routinely ageing lobsters, and the lack of information on the size-frequency from the landings and the nature of a stock-recruitment relationship. While a dynamic surplus production model has been applied to the data, an implicit assumption about the form of the stock recruitment relationship is required (Polovina 1991).

A more general approach is to begin with a model which expresses N_t as the number of exploitable lobsters at time t as a function of N_{t-1} , Z as the total instantaneous mortality from time $t-1$ to t , and r as the number which recruit and survive from $t-1$ to t as

$$N_t = r + N_{t-1} e^{-Z}.$$

Using the relationship that the product of catchability (q) and $N_{(t)}$ is $CPUE_{(t)}$, this model becomes

$$CPUE_t = q * r + CPUE_{t-1} e^{-M-qf},$$

where M and f are annual instantaneous natural mortality and fishing effort, respectively, during the period $t-1$ to t . This CPUE model, a simple version of a size-structured model developed by Schnute et al. (1989), was used to estimate population parameters and to

evaluate the extent that fishing effort explains the observed variation in CPUE. This model assumes constant catchability and recruitment; hence, the differences between predicted and observed CPUE are interpreted as variation in recruitment, catchability, or both.

The commercial data do not indicate whether effort was directed at slipper or spiny lobster. However, the catches can be grouped into two periods based on the proportion of spiny to slipper lobsters. In period 1 (1983-84 and 1988-90), ~80% of the landings were spiny lobster; in period 2 (1985-87), ~56% of the landings were spiny lobster (Table 1). The change in proportion of spiny lobster catches is likely due to changes in targeting and abundance. The CPUE

model is modified so that a catchability coefficient can be estimated for each period. Our modified CPUE model regresses the CPUE of spiny lobster above the minimum size in month t ($CPUE_t$) on the CPUE of the same month in the previous year:

$$CPUE_t = R * Q_t e^{-\frac{(M+Q_t f_t)}{2}} + (CPUE_{t-12}) (e^{-M-Q_t f_t}) \left(\frac{Q_t}{Q_{t-12}} \right)$$

with

$$Q_t = q_1 I_{1,t} + q_2 I_{2,t}$$

where q_1 is the catchability of spiny lobster during period 1, q_2 is the catchability during period 2, M is the annual instantaneous natural mortality, R is the annual recruitment, f is the cumulative fishing effort during the period ($t-12$, $t-1$), and $I_{i,t}$ ($i=1,2$) is the indicator or set function which takes the value 1 if t is within period i or otherwise takes the value 0. Estimates of R , q_1 , q_2 , and M were obtained by minimizing the sum of squares of the difference between the square root of the observed and predicted CPUE with a simplex algorithm.

Sea level data

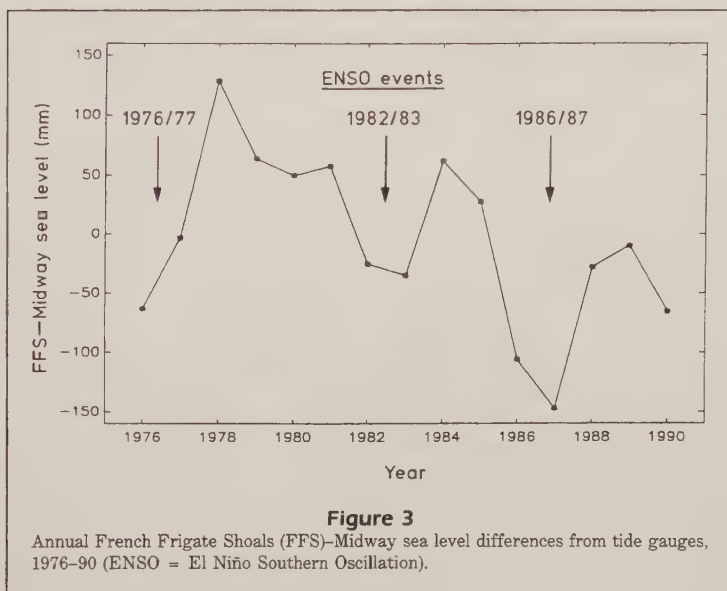
To examine the relationship between lobster recruitment variation at Maro Reef and physical factors such

as variation in the SCC, we focused on the analysis of sea level data from the NWHI. Our choice of sea level was primarily a practical one. In comparison to current or upper-layer temperature records, the sea level records are of long duration, and the data are measured continuously and are available in nearly real-time. An additional advantage is that sea-surface height data from the Geosat satellite altimeter are available to provide a spatial description that complements the temporal description available from the sea level stations.

Data on the difference in sea level between the gauges at French Frigate Shoals (FFS) and at Midway Is. have been available since 1976 (Figs. 1, 3). This sea level difference (denoted as FFS-Midway sea level) serves as an index of the geostrophic current anomalies across the NWHI in the region of Maro Reef. For example, an increase in the sea level height at FFS relative to Midway Is., measured from tide gauges, indicates the strengthening of a current that is across the gradient between the two locations and is flowing from the southwest to the northeast.

To interpret these flow anomalies as a manifestation of the variations in SCC strength, the spatial structure of the sea-surface height variation was examined by mapping the variability observed by the Geosat altimeter during November 1986–November 1988. These 2 years were selected because more accurate orbit estimates were available during this time-period and would result in more accurate sea-surface height fields. The Geosat geophysical data records were obtained from NOAA (Cheney et al. 1987) and were processed with software developed at the University of Hawaii.

Averages of the Geosat data over November 1986–November 1987 were subtracted from the averages over November 1987–November 1988. Before using the Geosat data, we checked that the resulting sea level differences from the altimeter were consistent with the corresponding sea level differences from tide gauges at FFS and Midway (not shown). Choosing these time-periods also allowed us to contrast conditions during the ENSO period of 1986–87, when the FFS–Midway sea level was low (~ 520 mm), with conditions during the normal period of 1987–88, when the FFS–Midway sea level was higher (~ 600 mm).



Puerulus settlement

During the last planktonic stage (i.e., postlarval or puerulus stage), spiny lobster acquire the benthic morphological features of adults and become active swimmers seeking benthic habitat. MacDonald (1986) studied puerulus settlement in the Hawaiian Archipelago with traps known as Witham Collectors at Kure Atoll (north of Midway Is.) in 1979–83 and at FFS in 1981–85. He computed mean catch per collector over 12-month periods (June–May) at Kure Atoll and FFS. These data will be compared with the FFS–Midway sea level data.

Results

The fit of the model to the commercial CPUE data and the resulting residuals indicate the model fits the trend in CPUE, but considerable unexplained variation exists in CPUE within and between years (Fig. 4). For example, given the fishing effort, CPUE was greater than expected in 1988 but declined more than expected in 1990. Since the model assumes both constant recruitment and constant catchability, the residuals may reflect variation in these factors. From the fit of the model, $R = 1.2 \times 10^6$ adult lobsters/yr, $M = 0.71/\text{yr}$, $q_1 = 1.2 \times 10^{-6}$, and $q_2 = 0.6 \times 10^{-6}$. Thus 1.2 million lobsters recruit to the fishery annually; with an M of 0.71/yr, only 50% of the 3-year-olds survive 1 year (in

the absence of fishing). Further, a CPUE of 1.2 spiny lobster/trap-haul means the exploitable population is 1 million spiny lobster. An independent estimate of M

from tagging at FFS is 0.5/yr (MacDonald 1984).

Commercial trapping effort since 1985 has averaged about 1 million trap-hauls (Table 1); using the q_1 estimate as catchability, annual fishing mortality (F) is estimated as 1.2/yr or $1.7 \times M$. With these figures and the estimates of growth and age at onset of sexual maturity, the Beverton-Holt yield equation estimates the spawning-stock biomass per recruit, when effort is 1 million trap-hauls, is 40% of what it would be in the absence of fishing (Polovina 1991). Thus, the ratio of F to M and the relative spawning-stock biomass calculations suggest that the spawning biomass in 1985–86 was not fished down to a level that would cause the poor recruitment to the fishery 4 years later (1989–90).

Much of the variation in residuals from the CPUE model is due to variation in recruitment at Maro Reef. For example, for the entire NWHI in 1990, trapping effort increased 11% from the previous year while the catch declined 33%, resulting in a 39% decline in CPUE. However, the decline in CPUE was most striking at Maro Reef, where CPUE declined 42% even though effort decreased by 37%. At Necker I., CPUE also declined (40%) but effort increased 35%.

The estimated age-frequency distributions based on research cruises at Maro Reef show a strong 3-year-old class in 1988 and a striking absence of all age-classes in 1990 (Fig. 5). This is consistent with the hypothesis that recruitment of the 3-year-olds to the fishery was weak in 1990 and subsequent fishing reduced all older age-classes. Necker I. had many more 2-year-olds in the samples since some trapping sites include nursery habitat; but between years, the abundance of 2-year-olds was relatively constant, whereas older lobsters declined in 1990, likely because of the increase in fishing effort (Fig. 6).

The NWHI lobster fleet is very mobile and shifts its trapping locations according to abundance of lobsters. By 1985, both Maro

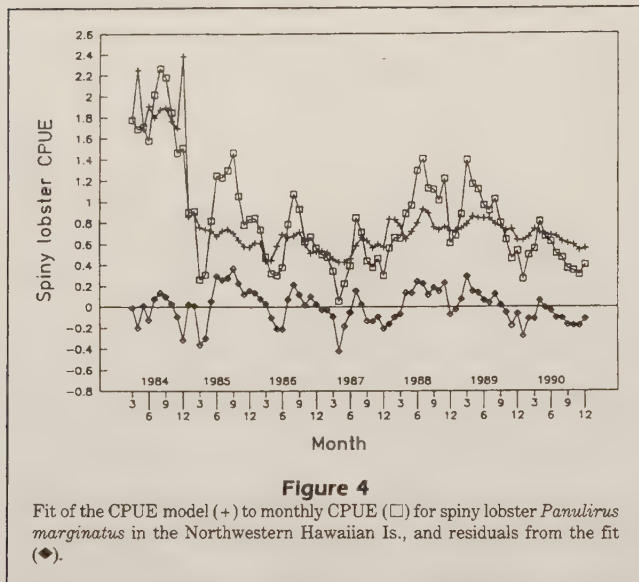


Figure 4

Fit of the CPUE model (+) to monthly CPUE (□) for spiny lobster *Panulirus marginatus* in the Northwestern Hawaiian Is., and residuals from the fit (◆).

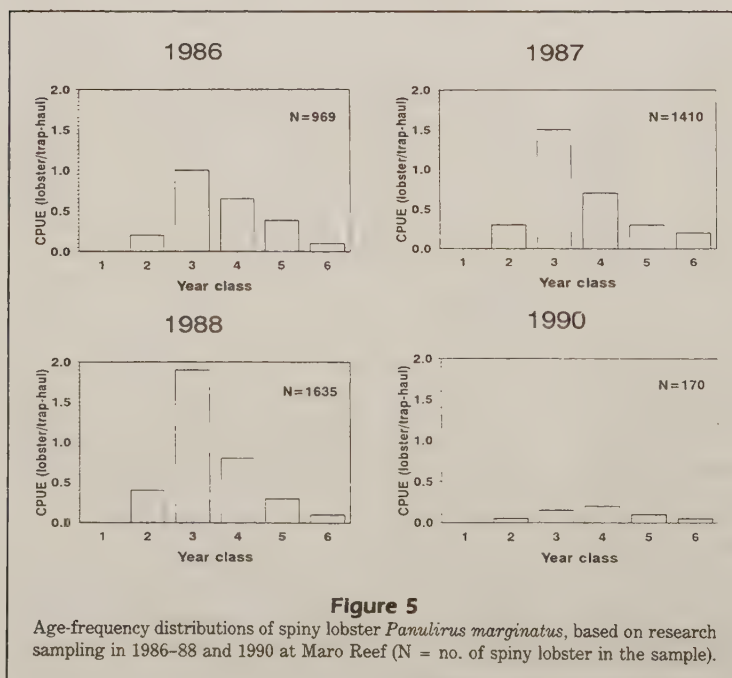


Figure 5

Age-frequency distributions of spiny lobster *Panulirus marginatus*, based on research sampling in 1986–88 and 1990 at Maro Reef (N = no. of spiny lobster in the sample).

Reef and Necker I. had gone through a period of fishing down the pre-exploitation population; the relative change in catches between the two banks may reflect changes in their relative recruitment. Since both banks are not always fished each month, we pooled the catches by quarter. A 3-quarter moving average of the ratio of quarterly catches at Maro Reef to the combined quarterly catches at Necker I. and Maro Reef shows considerable variation (Fig. 7). For example, catches from Maro in 1985 and 1988 represented almost 80% of the catches from the two banks, but in 1990 they represented less than 20%. A 3-quarter moving average of the residuals from the CPUE model shows the same trend as the ratio of catches from Maro Reef relative to Necker I. and Maro Reef combined (Fig. 7). This suggests that the variation in recruitment, catchability, or both at Maro Reef is responsible for most of the variation not explained by fishing effort observed for the entire NWHI.

height of the sea level ridge stretching across the Pacific. The height and location of this sea level ridge

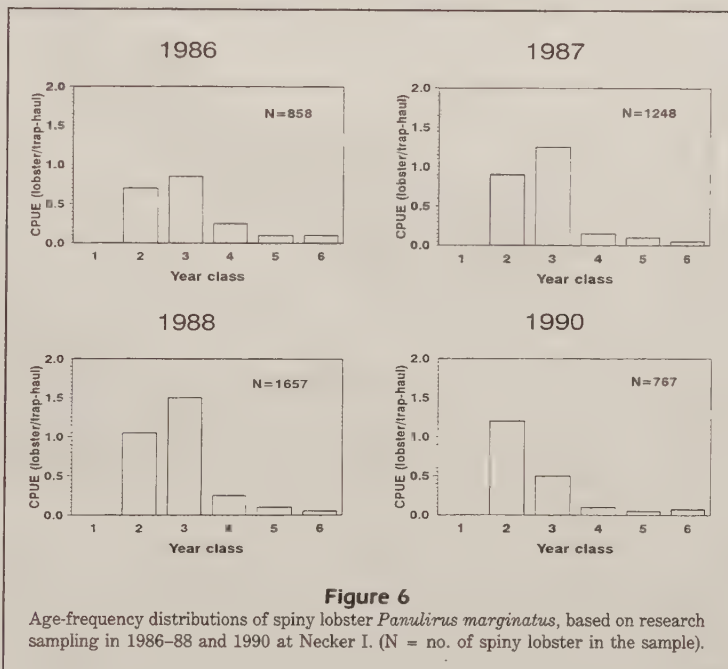


Figure 6

Age-frequency distributions of spiny lobster *Panulirus marginatus*, based on research sampling in 1986–88 and 1990 at Necker I. (N = no. of spiny lobster in the sample).

Variation between sea level and the SCC

Differences in sea level over the Pacific, between a year when the FFS–Midway sea level was high and a year when it was low, appear as a ridge of positive values, extending from southwest to northeast, that parallels a trough of negative values to the northwest (Fig. 8). Midway lies in the trough, Honolulu is on the ridge, and FFS lies on the gradient, which corresponds to the region of the most energetic geostrophic flow anomalies. This ridge and trough indicate that the change in the FFS–Midway sea level from low to high reflects the increase in a ridge extending across the western Pacific. The increase in the ridge and trough pattern represents an increase in the current flow along the gradient of this ridge. The path of this gradient or flow across the Pacific is consistent with the general path of the SCC. Thus FFS–Midway sea level measures a large-scale oceanographic feature which is represented by the

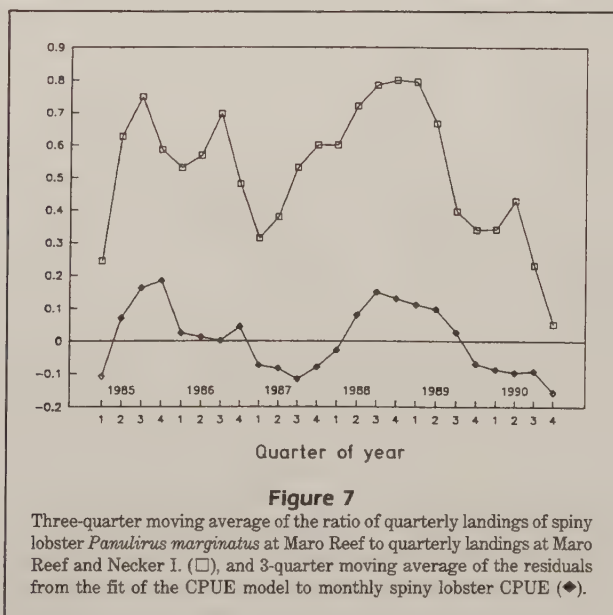


Figure 7

Three-quarter moving average of the ratio of quarterly landings of spiny lobster *Panulirus marginatus* at Maro Reef to quarterly landings at Maro Reef and Necker I. (□), and 3-quarter moving average of the residuals from the fit of the CPUE model to monthly spiny lobster CPUE (◆).

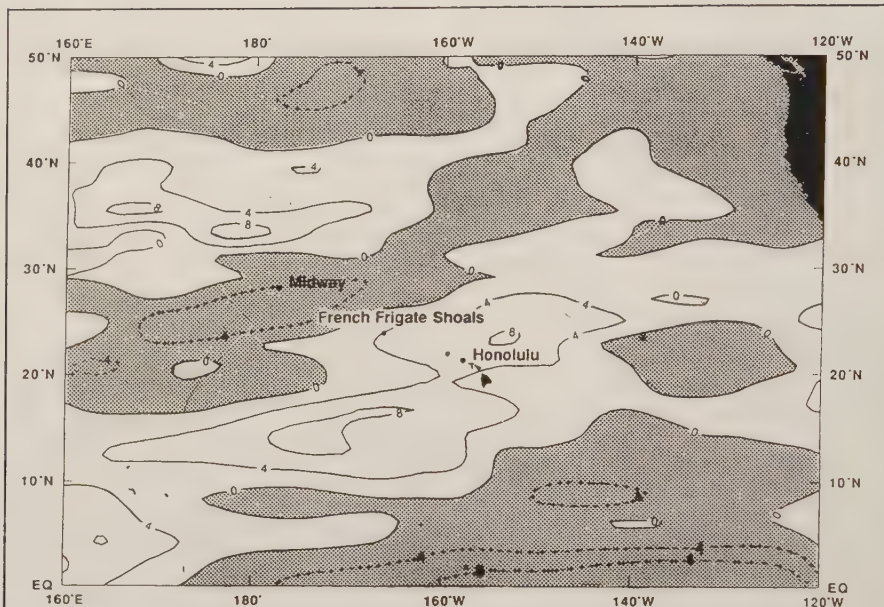


Figure 8

Differences between mean sea level during a non-ENSO (El Niño Southern Oscillation) period (Nov. 1987–Sept. 1988) and an ENSO period (Nov. 1986–Sept. 1987) from Geosat data. Negative values denoted by shaded areas.

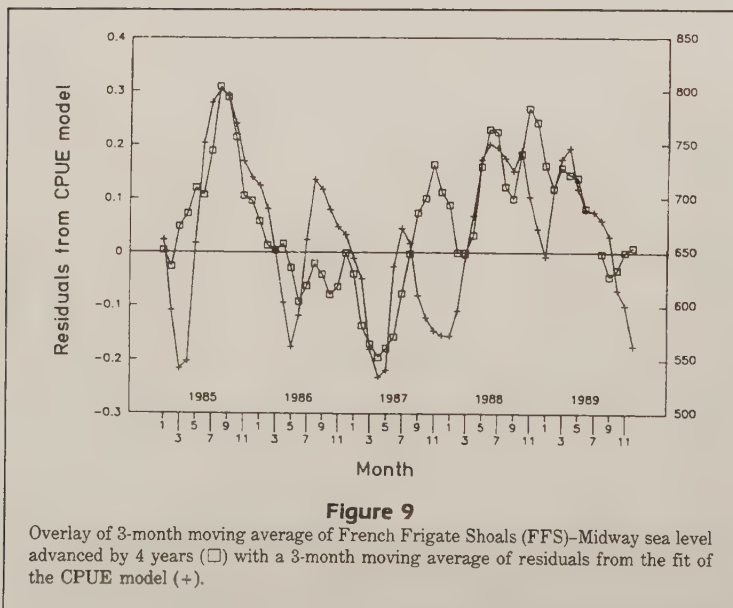


Figure 9

Overlay of 3-month moving average of French Frigate Shoals (FFS)–Midway sea level advanced by 4 years (□) with a 3-month moving average of residuals from the fit of the CPUE model (+).

correspond to the SCC strength and position, respectively.

Relationship between sea level and lobster abundance

Lagged cross-correlations between FFS–Midway sea level and the variables (i.e., the ratio of catches at Maro Reef to the combined catches at Maro Reef and Necker I., and the residuals from the CPUE model) have their strongest correlations (r 0.82 and 0.68, respectively) with sea level lagged by exactly 4 years. When sea level is lagged by 4 years and overlaid with these time-series, there is good agreement (Figs. 9, 10). Based on research samples pooled over 1986–88, the mean estimated age of lobsters caught by the fishery is 3.8 years (after settlement).

Based on the comparison of FFS–Midway sea level with the available puerulus settlement data from MacDonald (1986) in the same year, the FFS–Midway sea level correlates positively with mean puerulus catches at Kure Atoll (r 0.78, P 0.11) and shows no significant correlation with mean puerulus catches at FFS (r -0.37, $P > 0.25$) (Fig. 11).

Discussion

The research and commercial catch and effort data presented here show that the recruitment of 3-year-old spiny lobster to the fishery has varied considerably at Maro Reef but has remained stable at Necker I., 670 km to the southeast. Fishing effort is not considered sufficiently heavy to explain a decline in recruitment, especially a decline at one bank and not the other. The relationship between recruitment to the fishery at Maro Reef and the FFS–Midway sea level advanced by 4 years suggests that environmental factors impacting the larval stage are responsible for the recruitment variation. The Geosat data suggest that the FFS–Midway sea level measures the SCC. Hence the SCC strength or location dictates recruitment strength to the fishery 4 years later. Consistent with this hypothesis is the mean age of lobsters in the commercial catches as well as the correlation between puerulus settlement at Kure Atoll and FFS–Midway sea level. The lack of correlation between puerulus settlement at FFS and sea level is consistent with the observation that recruitment at the lower end of the NWHI is not linked to the same pattern of variation as Maro Reef. Annual variation in both SCC strength and position has been observed in the western Pacific (White and Hasunuma 1982). In summary, the temporal pattern of spiny lobster recruit-

ment differs between Necker I. and Maro Reef. At Maro Reef, large-scale oceanographic features appear to control the abundance of late-stage larvae, which in turn results in interannual variation in recruitment to the fishery.

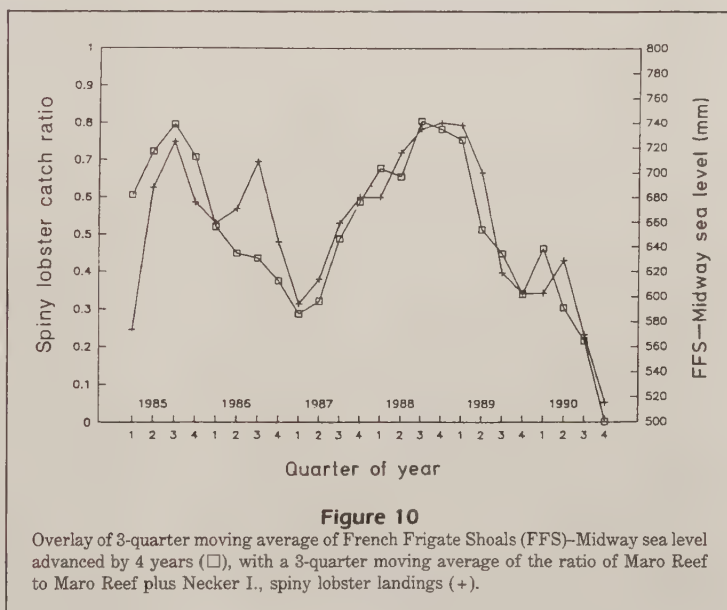


Figure 10

Overlay of 3-quarter moving average of French Frigate Shoals (FFS)–Midway sea level advanced by 4 years (□), with a 3-quarter moving average of the ratio of Maro Reef to Maro Reef plus Necker I., spiny lobster landings (+).

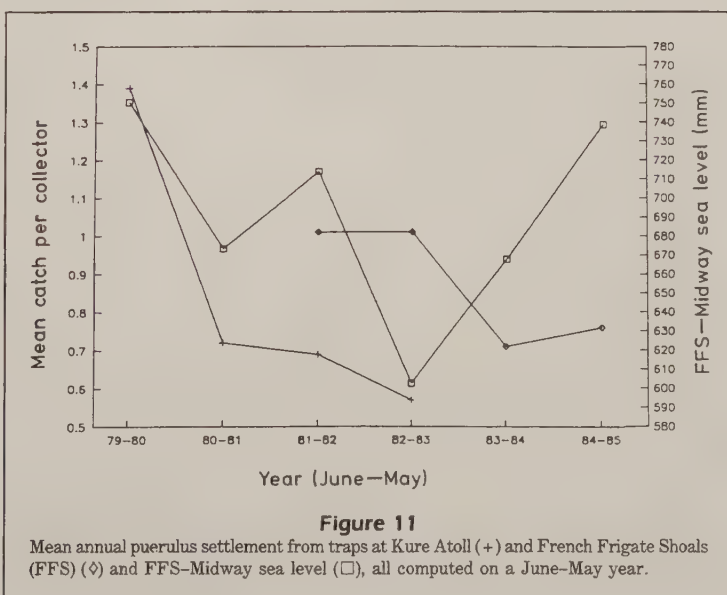


Figure 11

Mean annual puerulus settlement from traps at Kure Atoll (+) and French Frigate Shoals (FFS) (◇) and FFS–Midway sea level (□), all computed on a June–May year.

The underlying mechanism linking the correlation between the SCC and subsequent recruitment at Maro Reef is not known. It is possible that the SCC returns larvae, which have been advected west of the archipelago, back to Maro Reef. The SCC has been hypothesized to transport *Acropora* coral from Johnston Atoll (lat. 16°45'N., long. 169°31'W) to FFS (Grigg 1982). In addition, larvae of a spiny lobster species not recorded as an adult in Hawaii have been transported from the Marshall Is. to the Hawaiian Archipelago (Phillips and McWilliam 1989).

However, it may be that the SCC impacts not advection but larval survival. Laboratory studies have shown that spiny lobster larvae suffer a high level of mortality when water temperatures drop below 20°C (T. Kazama, NMFS Honolulu Lab., pers. commun., Sept. 1991). In the years we estimated that the SCC was weak, water temperatures <20°C in the winter have been observed at Maro Reef but not Necker I. If little larval mixing occurs between Maro Reef and Necker I., larval mortality at Maro Reef resulting from low winter temperatures could account for the observed recruitment variation.

A third hypothesis is that when the SCC has a particular speed and location, it produces fronts which retain larvae near Maro Reef. When the SCC is weak or shifts, these fronts are not formed near Maro Reef. Preliminary evidence from the drifter buoys and larval sampling in our study suggests fronts north of Maro Reef and south of Necker I. may be important for lobster larvae (Polovina, pers. observ.)

One potential management application of the lagged relationship between FFS-Midway sea level and recruitment is that it provides up to a 4-year forecast of recruitment to the fishery at Maro Reef. A 3-quarter moving average of the FFS-Midway sea level shifted forward by 4 years forecasts poor recruitment in 1991, followed by an improvement beginning in late 1992 (Fig. 12). During January-May 1991 before the fishery was closed for 6 months, recruitment at Maro Reef clearly had not recovered, as only 1052 spiny lobster were harvested from Maro Reef while 34,746 spiny lobster were harvested from Necker I. Recall that the relative catches between banks provide an index of relative abundance, since the fleet moves to maximize the CPUE. The FFS-Midway sea level data forecast that catches at Maro Reef will improve beginning in late 1992 (Fig. 12). Data from larval tows are consistent with this forecast. Standardized larval tows, taken in June and November 1989 over a grid of stations from the 200 m isobath out to 56 km around both Necker I. and Maro Reef, caught 3802 and 3342 late-stage phyllosomes, respectively (J. Polovina, unpubl. data). A *t*-test, based on a lognormal distribution, finds no significant difference in the mean abundance of larvae between Maro Reef and Necker I. If we assume that larval abundance was high around Necker I. in 1989, then good larval recruitment apparently has returned to Maro Reef. This is consistent with the observed higher sea-level values in 1989 (shown as 1993 values in Fig. 12, since the sea level has been advanced by 4 years) and suggests that catches will be high at Maro Reef in 1993.

The FFS-Midway sea level time-series from 1976 to 1990 (Fig. 3) shows that ENSO events may result in poor recruitment to the fishery 4 years later, but the series also shows a long-term decline. Reasons for the low FFS-Midway sea level during ENSO events are not known, but may be related to a decrease in surface water supplied to the SCC in the western Pacific. Such a change could be associated with the circulation disruptions observed in the tropical Pacific during ENSO events (Meyers and Donguy 1984). The long-term decline in sea level from 1976 to 1990 suggests there is a low-frequency component in the variation in SCC strength and, hence, lobster recruitment. Thus, it may be some time before recruitment to the fishery is at the early 1980s' level.

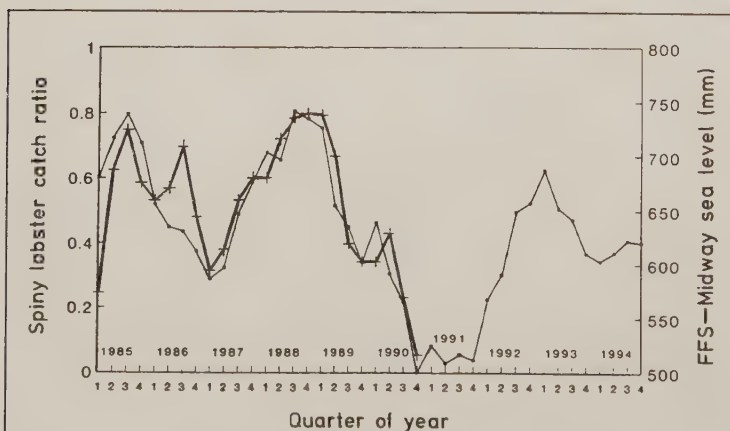


Figure 12

Three-quarter moving average of the ratio of quarterly landings of spiny lobster *Panulirus marginatus* at Maro Reef to quarterly landings at Maro Reef and Necker I. (bold line) overlaid with the 3-quarter moving average of French Frigate Shoals (FFS)-Midway sea level deviation advanced by 4 years (thin line).

Acknowledgments

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Abstract. — A deepwater trapping survey for *Heterocarpus laevigatus* was conducted around the main islands of the Hawaiian Archipelago to estimate exploitable biomass and potential yield. Stratified sampling by depth zone and island was conducted over a 3-year period to evaluate shrimp catch rates. Catchability of the traps was estimated from a 12-day intensive fishing experiment performed at a small, isolated site in the Kaulakahi Channel; habitat areas were determined by digitizing nautical charts.

Results from a Leslie analysis of the depletion experiment showed that *H. laevigatus* is very susceptible to capture by traps (i.e., catchability $q = 9.48 \text{ ha/trap-night}$). There was no evidence of a change in size structure through the course of the experiment.

Shrimp catch rates varied greatly by island and depth of capture. Exploitable biomass was greatest in the 460–640 m depth range; negligible amounts of shrimp occurred shallower than 350 m and deeper than 830 m. Catch rates were highest at Niihau and lowest at Oahu. The total exploitable biomass of shrimp in the main Hawaiian Is. was estimated to be 271 MT, a figure substantially less than previously believed.

Analysis of multiple size-frequency distributions for each sex showed no evidence of modal size progression. Assuming equilibrium conditions, application of the Wetherall et al. (1987) method to these data resulted in estimates of $M/K = 1.01$ for female shrimp and 0.74 for males. From these results and estimates of L_{∞} we calculate that $F_{0.1}/M = 0.75$ for females and 0.86 for males.

An assessment of the exploitable biomass of *Heterocarpus laevigatus* in the main Hawaiian Islands. Part 1: Trapping surveys, depletion experiment, and length structure

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The caridean shrimp, *Heterocarpus laevigatus* Bate 1888, is an abundant deepwater inhabitant of the Hawaiian Is., where it has been fished sporadically since 1970 (Anon. 1979). Two early research surveys (Clarke 1972, Struhsaker and Aasted 1974) showed that large catches of this species, and its smaller congener *H. ensifer*, could readily be taken in baited traps in water depths of 365–825 m (200–450 fm).^{*} Based on catch rates from around the island of Oahu, the deepwater shrimp resource seemed sufficiently abundant to support a commercial fishery (2.6 kg/trap-night for *H. laevigatus* and 6.6 kg/trap-night for *H. ensifer*; Struhsaker and Aasted 1974).

To date, however, attempts to harvest the resource have met with limited success, even though 75 MT of *H. laevigatus* were landed by one vessel during a 14-month period (Tagami and Barrows 1988). At its peak in 1983–84, a short-lived fishery developed, involving as many as 7 medium-sized (23–40 m) boats. At that time over 190 MT of *H. laevigatus*

were landed, with an ex-vessel value of \$1.5 million (\$7.85/kg; Hawaii Dep. Land & Nat. Resour., Div. Aquat. Resour.). The fishery soon failed, however, primarily due to problems with gear loss, product processing, and localized stock depletions. Even so, the product was well received by the public, and rejuvenating the shrimp fishery remains a fishery development goal of the State of Hawaii (Anon. 1984).

With this interest in developing the Hawaiian fishery, major gaps in our knowledge of local *H. laevigatus* shrimp stocks have become apparent (see Gooding 1984, Dailey and Ralston 1986), although elsewhere in the Pacific more extensive data are available (e.g., Wilder 1977, King 1984 and 1986, Ralston 1986, Moffitt and Polovina 1987). Particularly lacking are estimates of the absolute abundance of the *H. laevigatus* stock in Hawaii and its ability to withstand sustained fishing pressure.

The primary objective of the work presented here was to estimate the exploitable biomass of *H. laevigatus* in the main Hawaiian Is. A secondary objective was to estimate growth and mortality rates through analysis of length-frequency data. Together

^{*}Depths are given in meters with fathom equivalents (1.0 fm = 1.83 m), although contouring and stratification were based on nautical charts in fathoms.

these findings could form a basis for estimating the potential yield of the shrimp resource.

To determine the exploitable biomass of shrimp at spatially discrete locations in Hawaii, the formula (Ricker 1975) was used:

$$CPUE = q \left[\frac{B}{A} \right]$$

where CPUE is the catch-per-unit-effort, q is the catchability coefficient of the fishing gear, B is exploitable biomass, and A is the area occupied by the population. This relationship is based on the explicit assumption that catch rate is strictly proportional to shrimp density (B/A), and that q is the proportionality constant equating these quantities. By rearrangement we have,

$$B = \frac{CPUE \cdot A}{q}$$

Thus, to estimate the exploitable shrimp biomass at a locality we need (1) an unbiased estimate of catch rate, (2) a measure of the habitat area over which the catch rate prevails, and (3) knowledge of the sampling gear's efficiency (i.e., an estimate of q).

To accomplish these three objectives, the study was divided into two phases. First, a depletion experiment was conducted to estimate the catchability coefficient (q). This was followed by a depth-stratified sampling program for *H. laevis* around each of the main islands of the Hawaiian archipelago (i.e., Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau).

Methods

Shrimp trapping was conducted during a series of nine cruises of the NOAA ship *Townsend Cromwell* (Table 1). During each cruise, standard fishing gear was utilized to gather CPUE statistics at specific geographical locations. The gear employed was a top-loading pyramidal shrimp trap, identical in construction to those used commercially in Hawaii from 1983 to 1984. Each trap was made of welded steel reinforcement bars, had a 1.83 m² base, an overall volume of 1.84 m³, and was covered by 1.27 × 2.54 cm mesh hardware cloth. A full description and illustration of the gear is given in Tagami and Barrows (1988).

Typically, 6–10 solitary traps were set daily and allowed to soak overnight. Traps were generally deployed in the afternoon and hauled the following morning, being in the water for a period of 16–20 hours. All traps were baited with approximately 3 kg of chopped mackerel *Scomber japonicus*. After hauling to the sur-

Table 1
Summary of shrimp-trapping cruise dates and locations.

Date	Location	No. of traps hauled
April 1985	Molokai	3
	Lanai	1
May 1986	Kaulakahi Channel	105
July 1986	Kaulakahi Channel	10
Sept. 1986	Kaulakahi Channel	10
Nov. 1986	Kaulakahi Channel	12
Sept./Oct. 1987	Niihau	68
	Kauai	128
	Kaulakahi Channel	11
Feb./March 1988	Kaulakahi Channel	10
	Oahu	8
	Hawaii	31
Oct. 1988	Kaulakahi Channel	17
	Molokai	20
	Lanai	18
	Maui	38
	Kahoolawe	8
March 1989	Oahu	67
	Molokai	32

face, each trap was emptied and the contents were sorted to species, counted, and weighed to the nearest 0.01 kg. Random subsamples of ~200 *H. laevis* were routinely collected, from which carapace length (CL) was measured to the nearest 0.1 mm using dial calipers. For all measured shrimp, sex was determined by examining the endopodite of the first pleopod (spatulate in males, pinnate in females; see King and Moffitt 1984). In addition, the ovigerous condition of females was recorded.

Depletion experiment

To estimate q , an intensive fishing experiment was conducted (see also Ralston 1986). Depletion experiments, including the Leslie method used here (Ricker 1975), have three restrictive assumptions. First, all individuals in the exploitable portion of the population are equally likely to be captured with the fishing gear. Second, the fished population is closed, or else additions exactly balance removals other than those due to fishing. Third, fishing removals account for all changes in stock biomass, such that natural mortality, growth, and recruitment have negligible effects during the period of fishing. Thus, the best site for a depletion experiment is a naturally isolated, small area so that removals can be carried out over as short a time-interval as possible.

A small rise midway in the Kaulakahi Channel (21° 54.5'N, 159° 56.5'W) separating Kauai and Niihau was

chosen for the work. This nearly circular rise (Fig. 1) with a crest at 421 m (230 fm), has an area of 1187 ha (horizontal planar area <640 m or 350 fm) and is isolated from the Islands of Kauai and Niihau by depths >730 m (400 fm; Fig. 2). The site lies in the required depth range for *H. laevisgatus* and has relatively high densities of the target species.

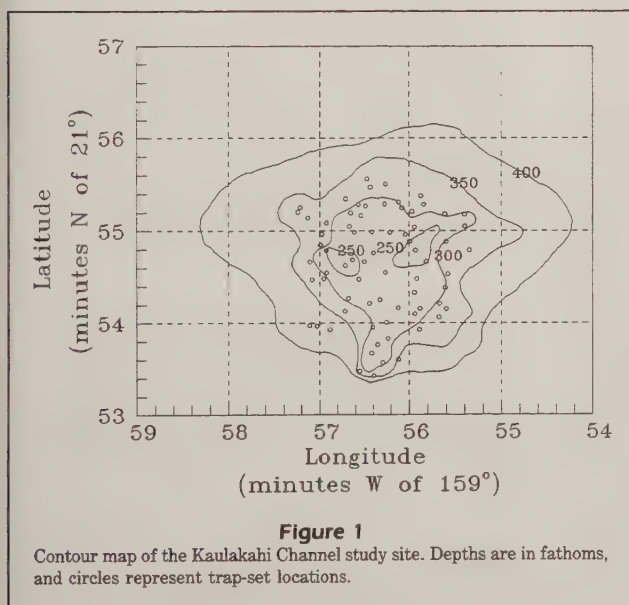


Figure 1

Contour map of the Kaulakahi Channel study site. Depths are in fathoms, and circles represent trap-set locations.

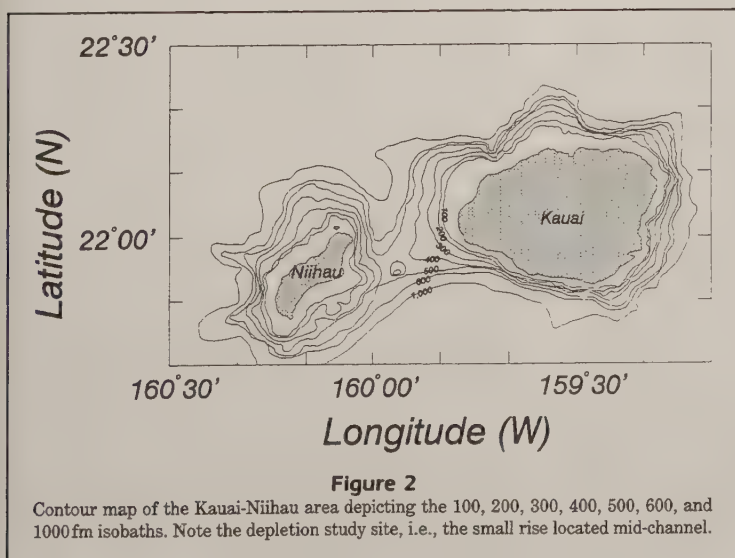


Figure 2

Contour map of the Kauai-Niihau area depicting the 100, 200, 300, 400, 500, 600, and 1000 fm isobaths. Note the depletion study site, i.e., the small rise located mid-channel.

The intensive fishing experiment was conducted 13–24 May 1986. During each of the 12 days of the experiment, 6–14 pyramidal shrimp traps were set between depths of 421 and 695 m (230 and 380 fm). Following the Leslie method (Ricker 1975, Seber 1982), catchability was estimated directly from the slope of the linear regression of CPUE on corrected cumulative catch. That is,

$$\begin{aligned} \text{CPUE}_i &= q \cdot B_i \\ &= q(B_0 - K_i) \\ &= qB_0 - qK_i, \end{aligned}$$

where CPUE_i is the catch-per-unit-effort on day i (kg/trap-night), q is the catchability coefficient/trap-night of the pyramid traps, B_i is the average biomass (kg) present on day i , B_0 is the biomass (kg) of shrimp present at the start of the experiment, and K_i is the corrected cumulative removals for day i , defined as

$$K_i = \frac{1}{2} C_i + \sum_{n=1}^{i-1} C_n,$$

where C_n ($n=1, 2, \dots, i$) is the catch (kg) taken on each day of the experiment. Note that the estimate of catchability (q) pertains strictly to the interaction between the traps we used and the stock resident in the study area, which is normalized to unit area after multiplying by 1187 ha (i.e., the area of the study site).

Determination of habitat areas

The distribution of *H. laevisgatus* is strongly dependent on bottom depth. Little or no shrimp occur in waters outside the 366–915 m (200–500 fm) range (Struhsaker and Aasted 1974, Gooding 1984, Dailey and Ralston 1986). In the main portion of the Hawaiian Archipelago (Hawaii, Maui, Lanai, Kahoolawe, Molokai, Oahu, Kauai, and Niihau) a number of islands share a common 915 m (500 fm) depth contour (e.g., Kauai and Niihau; Fig. 2). Even so, in our study each island was treated as a separate stock for

purposes of geographically stratifying the analysis. An exception was made for the islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM), which share, in addition to the 915 m (500 fm) contour, a common 366 m (200 fm) isobath. These four islands were, therefore, treated as a single geographic locality.

Estimates of the amount of suitable shrimp habitat, in hectares (1 ha = 0.01 km²), were obtained by determining the horizontal planar area lying between charted depth contours. A large digitizing tablet was used to calculate all area estimates directly from nautical charts (NOAA charts 19016, 19019, and 19022, and Defense Mapping Agency bottom contour charts). These charts included 915 m (500 fm) isobaths, but we manually contoured all of the 366 m (200 fm) isobaths using the sounding data provided on each chart. In addition, good detailed bathymetry was available for the islands of Kauai and Niihau, and at these sites the 458 m (250 fm), 549 m (300 fm), 640 m (350 fm), 732 m (400 fm), and 824 m (450 fm) isobaths were contoured and digitized as well.

Each contour was digitized three times by each author, providing a minimum estimate of measurement error in our calculation of habitat areas. These errors were typically small (median CV 0.5%, range 0.1–1.9%). A potentially more serious type of error concerns discrepancies between the actual locations of contours and their representations on charts. However, we had no information concerning the magnitude of this type of error and, given that measurement errors were negligible, we assumed that our estimates of habitat area were accurate and precise.

These data were then used to calculate habitat areas for each 92 m (50 fm) depth interval between 366 and 915 m (200–500 fm). First, the relative distribution of habitat was calculated from the Kauai and Niihau data. To estimate depth-specific habitat areas for the three remaining sites (Oahu, MLKM, and Hawaii), the combined relative proportions of habitat for each depth interval obtained at Kauai–Niihau were applied to the estimates of total habitat area between 366 and 915 m (200–500 fm). In support of this procedure, results in Mark and Moore (1987) indicate that slope-depth relationships among the main islands of the archipelago are, in general, similar.

Depth-stratified sampling

For the second phase of the assessment, each of the island areas was targeted for comprehensive trapping surveys to determine abundance patterns (i.e., catch rate) with depth and to estimate standing stocks (Table 1). A depth-stratified sampling approach was used. From preliminary data gathered at Kauai and Niihau during the September 1987 cruise, the mean and vari-

ance in CPUE were calculated for each of the six 92 m (50 fm) depth intervals lying in the 366–915 m (200–500 fm) range. Based on the results of this vertical distribution survey, sampling effort was optimally partitioned into depth strata by Neyman allocation (Cochran 1977), i.e., trap allocations to each depth interval were based on the product of abundance (CPUE · habitat area) and the standard deviation of CPUE at that depth. As each cruise progressed, CPUE means and variances were recalculated daily and the trap allocation schedule was updated.

From the results of the surveys, exploitable biomass was estimated (Eq. 1) for each depth interval at each site visited. This calculation assumes that the catchability estimate, which was determined at the depletion experiment study site, can be extended to all other localities sampled. An estimate of the variance of the biomass for each stratum was obtained from Eq. 1 using the delta method (Seber 1982), resulting in

$$\text{VAR}[B] \approx \frac{A^2}{\hat{q}^2} \text{VAR}[\text{CPUE}] + \frac{A^2 \cdot \text{CPUE}^2}{\hat{q}^4} \text{VAR}[\hat{q}]$$

if all covariance terms are zero (a reasonable first assumption) and VAR[A] is negligible (see above). Confidence intervals were then calculated using the distribution of standard normal scores ($\alpha = 0.05$, $Z = 1.96$).

Length-frequency analysis

The Kaulakahi Channel experimental depletion site was visited on seven separate occasions during May 1986–March 1988 (Table 1). During each visit a length-frequency sample of *H. laevigatus* was obtained, with the ultimate goal of analyzing the progression of size modes over time (egg bearing is strongly seasonal; Dailey and Ralston 1986, Moffitt and Polovina 1987). Additional length-frequency samples were obtained during the course of the depth-stratified sampling at each of the island sites.

Mortality and growth parameters were estimated from length-frequency distributions using the regression method of Wetherall et al. (1987). This technique requires an equilibrium population size-structure, an undesirable and restrictive assumption. Even so, data are available to support its use. Dailey and Ralston (1986) present length-frequency data for male and female shrimp sampled during the earliest stages of the fishery (1983–84). The data are very similar to those presented here, suggesting that exploitation has yet to seriously affect size composition. Additionally, the time-invariance of the size-frequency data we collected at the Kaulakahi study site (see below) indicates equilibrium conditions.

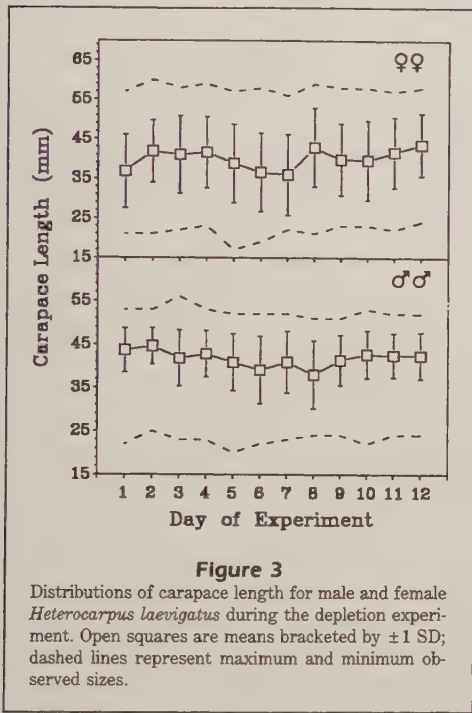


Figure 3

Distributions of carapace length for male and female *Heterocarpus laevis* during the depletion experiment. Open squares are means bracketed by ± 1 SD; dashed lines represent maximum and minimum observed sizes.

For each sex, the von Bertalanffy asymptotic length (CL_{∞}) and the ratio (Θ) of the total mortality rate (Z/yr) to the von Bertalanffy growth coefficient (K/yr) were estimated from a weighted regression of mean lengths ($CL_{\mu i}$) on full vulnerability cutoff lengths (CL_{ci}). In the analysis, the CL_{ci} were incremented in 1.0 mm steps above CL_{co} , the minimum size of full vulnerability to the gear, and the $CL_{\mu i}$ were recalculated at each step. Using the morphometric functional regressions presented in Dailey and Ralston (1986), CL_{co} was set equal to 30 mm (the length of *H. laevis* with carapace width = 12.7 mm), corresponding to the least dimension of the wire mesh covering the traps. This approach to estimating CL_{co} deviates from that used in previous applications of the regression method to *H. laevis* stocks. Dailey and Ralston (1986) and Moffitt and Polovina (1987) both assumed that shrimp were not fully selected by baited traps until reaching a CL greater than the modal size of length-frequency distributions from trap catches.

Because the size-structure we observed was similar to the unexploited stock (see above), it follows that $\Theta = M/K$, where M is natural mortality/yr. Likewise, using the length-weight regressions of Dailey and Ralston (1986), we estimated the asymptotic weights

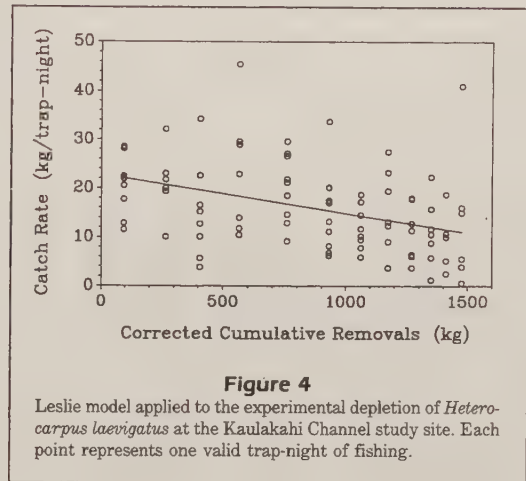


Figure 4

Leslie model applied to the experimental depletion of *Heterocarpus laevis* at the Kaulakahi Channel study site. Each point represents one valid trap-night of fishing.

(W_{∞}) for each sex as the predicted weight at $CL = CL_{\infty}$. The average size at entry to the fishery (CL_p , *sensu* Beverton and Holt 1957) was obtained by averaging the minimum size caught and CL_{co} . Given estimates of M/K , W_{∞} , and CL_p , we used the tables presented in Beverton and Holt (1966) to determine sex-specific values of yield-per-recruit (Y/R) at various levels of exploitation (F/M). From these data we computed values of $F_{0.1}/M$, the exploitation level at which the marginal increase in Y/R declines to 10% of its value at the origin (Gulland and Boerema 1973, Gulland 1983).

Results

Depletion experiment

During the depletion experiment, 123 pyramid shrimp traps were set at the Kaulakahi Channel study site. Of these, 19 were lost, resulting in 104 effective trap-nights of standard fishing effort and a gear loss rate of 15%. A total of 45,482 *H. laevis* were caught, which collectively weighed 1499 kg. The average size of each shrimp was therefore 33.0 g. During the 12-day course of the experiment, no change occurred in the daily mean size of shrimp caught (Fig. 3; $r_0 = 0.32$, $df\ 10$; $r_0 = -0.28$, $df\ 10$).

Individual trap catches were regressed on values of corrected cumulative removals to date (Fig. 4). Traps that did not fish properly (e.g., the funnel entrance was ajar upon retrieval) were not included, although cumulative removals (K_i) included all shrimp caught in the study area (<695 m or 380 fm). Therefore, each point represents an observation of CPUE from one valid

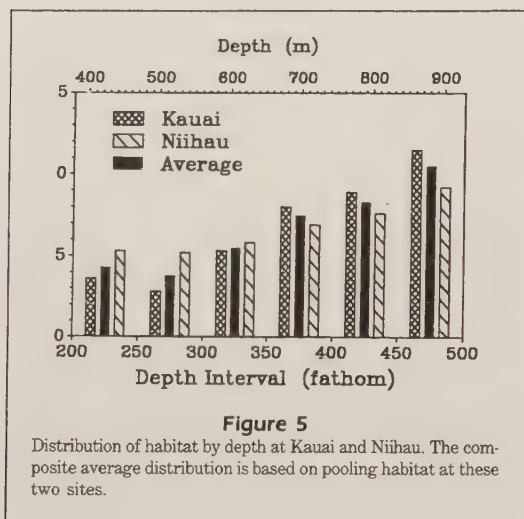


Figure 5

Distribution of habitat by depth at Kauai and Niihau. The composite average distribution is based on pooling habitat at these two sites.

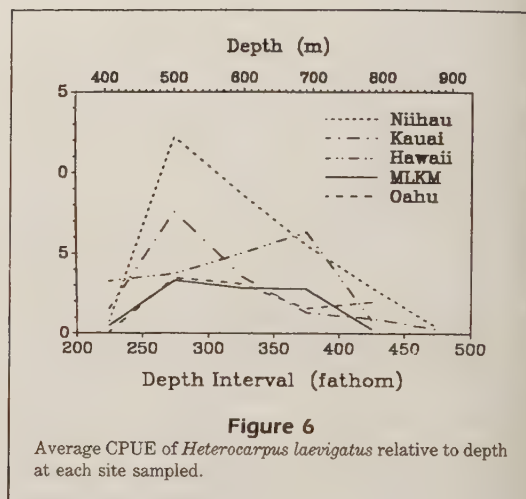


Figure 6

Average CPUE of *Heterocarpus laevis* relative to depth at each site sampled.

trap-night of fishing. Also presented is the ordinary least-squares regression equation relating these variables. The equation of the line is

$$\text{CPUE}_i = 22.84 - 0.007988[K_i],$$

with standard errors of the slope and intercept equal to 0.00197 and 1.9368, respectively. The regression is highly significant ($F_{1,89} = 16.00$, $P = 0.0001$). The residuals show no obvious departure from linearity, an indication of constant catchability.

Under the Leslie model, the exploitable biomass at the start of the experiment is defined by the x-intercept, i.e., 2859 kg. Because the study site covered 1187 ha, this amounts to an initial density of 2.4087 kg/ha, which produced an initial catch rate (CPUE_0) equal to 22.84 kg/trap-night (i.e., the y-intercept). Then, $\hat{q}$ expressed on a hectare basis, rather than defined in terms of the study site, is estimated to be 9.4798 ha/trap-night. In real terms, one overnight soak of a single, large pyramidal shrimp trap is estimated to have captured $\sim 0.8\%$ of the shrimp in the entire study area, which is equivalent to all the shrimp in ~ 9.5 ha, were they randomly dispersed. The standard error of $\hat{q}$ /ha is the product of A (1187 ha) and the standard error of $\hat{q}$ measured over the study site (0.00197) (Seber 1982).

It is instructive to note that an initial density of 2.4087 kg/ha is equivalent to an average of 73 shrimp/ha (see statistics for mean shrimp weight above). Based on this density, the average utilization of habitat by each shrimp was 137 m², a remarkable figure given

the relatively high catch rate encountered at the beginning of the depletion experiment (22.83 kg/trap-night).

Depth-stratified sampling

Habitat areas by 92 m (50 fm) depth intervals were estimated for the Oahu, Hawaii, and MLKM sites by assuming that the proportionate distribution of habitat between 366 and 915 m (200–500 fm) at these sites was the same as the composite distribution obtained at Kauai and Niihau. While there were some differences in the distribution of habitat with depth between Kauai and Niihau (Fig. 5, Table 2), they were relatively minor. At both sites the amount of habitat in the 458–549 m (250–300 fm) depth interval was slightly less than in the 366–458 m (200–250 fm) interval; but with increasing depth below that, the amount of habitat per 92 m (50 fm) depth interval increased steadily.

There were, however, marked differences in CPUE with depth among the five localities sampled (Fig. 6, Table 2). Catch rates at Niihau were particularly high relative to the other areas, especially at 458–549 m (250–300 fm). Catch rates at Oahu and MLKM were much lower. The modes of the distributions at Kauai and Niihau were shifted to the shallow end of the depth range, whereas at Hawaii it was shifted deeper.

Results presented in Table 2 provide estimates of the exploitable biomass (B), as well as variance estimates, for the depth intervals sampled at each site. Although catch rates at Niihau are quite high, the reduced amount of habitat at this island (69,530 ha) is sufficient to support only a small stock of shrimp (35.7 MT). Oahu, with its much lower catch rates, has a larger exploit-

Table 2
Depth-stratified sampling results for *Heterocarpus laevigatus* in the main Hawaiian Is.

Depth range		No. traps set	Mean CPUE kg/trap	VAR[CPUE]	Habitat area (ha)	B (kg)	VAR[B]
(m)	(fm)						
Kauai							
366-458	200-250	29	1.566	0.894	12,760	2,108	1,897,271
458-549	250-300	37	7.587	1.093	12,070	9,663	7,608,356
549-640	300-350	25	3.607	0.322	14,410	5,481	2,621,353
640-732	350-400	18	1.324	0.436	16,940	2,367	1,742,930
732-824	400-450	6	0.953	0.203	17,770	1,786	912,472
824-915	450-500	7	0.299	0.038	20,200	637	197,960
Totals		122			94,150	22,042	14,980,342
Niihau							
366-458	200-250	9	0.788	0.586	10,670	887	791,140
458-549	250-300	18	12.214	7.253	10,570	13,611	20,586,349
549-640	300-350	19	8.719	3.335	11,010	10,127	10,907,759
640-732	350-400	10	5.533	2.737	11,730	6,847	7,120,644
732-824	400-450	4	2.903	0.906	12,210	3,739	2,377,052
824-915	450-500	4	0.380	0.094	13,340	535	204,092
Totals		64			69,530	35,746	41,987,037
Oahu							
366-458	200-250	6	0.122	0.017	41,570	535	342,588
458-549	250-300	20	3.482	3.239	40,100	14,726	71,490,061
549-640	300-350	33	3.115	0.480	45,070	14,810	24,568,526
640-732	350-400	13	1.594	0.698	50,800	8,542	24,613,230
732-824	400-450	2	1.990	0.303	53,300	11,187	17,379,858
824-915	450-500	0	0.000	0.000	59,510	0	0
Totals		74			290,350	49,800	138,394,264
Hawaii							
366-458	200-250	1	3.270	2.152	38,720	13,357	47,049,206
458-549	250-300	4	3.750	2.223	37,320	14,767	48,097,991
549-640	300-350	11	5.008	3.882	41,980	22,171	106,796,660
640-732	350-400	11	6.325	3.036	47,300	31,560	137,841,468
732-824	400-450	4	0.858	0.889	49,630	4,491	25,603,225
824-915	450-500	0	0.000	0.000	55,430	0	0
Totals		31			270,350	86,345	365,388,550
Maui-Lanai-Kahoolawe-Molokai							
366-458	200-250	15	0.500	0.110	69,420	3,662	6,716,452
458-549	250-300	43	3.338	0.399	66,920	23,567	54,580,681
549-640	300-350	42	2.823	0.168	75,250	22,409	41,983,921
640-732	350-400	19	2.795	0.653	84,790	25,004	91,353,003
732-824	400-450	1	0.300	0.079	88,970	2,815	7,443,949
824-915	450-500	0	0.000	0.000	99,370	0	0
Totals		120			484,730	77,457	202,078,006

able biomass of *H. laevigatus* than does Niihau. In aggregate, we estimate the exploitable stock at all islands to be $B_{\Sigma \text{tot}} = 271.4 \text{ MT}$ ($p[217.3 \leq B_{\Sigma \text{tot}} \leq 325.5] = 0.95$, SE 27.6 MT, CV 10.18%).

Analysis of length-frequency data

Although the Kaulakahi Channel study site was sampled on seven different occasions over a 29-month period

(May 1986–October 1988), during which over 6800 female and 11,800 male shrimp were sexed and measured, there was little evidence of progression in size modes (Fig. 7). The CL frequency distributions of male shrimp were particularly stagnant, and those of females showed no coherent pattern that could be attributed to the influx of year-classes into the exploitable population.

Due to the apparent stationary behavior of these

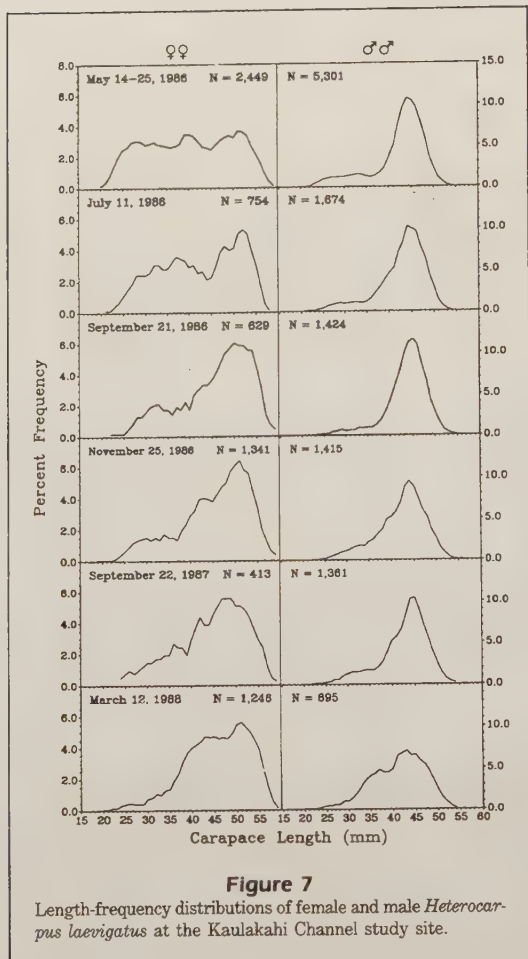


Figure 7

Length-frequency distributions of female and male *Heterocarpus laevis* at the Kaulakahi Channel study site.

distributions, all the length data were pooled (Fig. 8). It is evident from the figure that female shrimp reach substantially larger sizes than do males, in agreement with previously published work (Dailey and Ralston 1986, Moffitt and Polovina 1987). Superimposed on the combined length-frequency distributions of males and females is the estimated size of *H. laevis* when fully vulnerable to the traps (i.e., $CL_{\infty} = 30$ mm CL). The carapace width of shrimp this size is equal to 1.27 cm (0.5"), the minimum mesh size of the traps.

We applied the Wetherall et al. (1987) regression method to these length-frequency data and estimated that $\Theta_f = 1.01 \pm 0.052$ and $\Theta_m = 0.74 \pm 0.075$. For females we estimated that $CL_{\infty} = 58$ mm (SE 0.37) and for males $CL_{\infty} = 50$ mm (SE 0.44), corresponding to $W_{\infty} = 80$ g for females and 55 g for males.

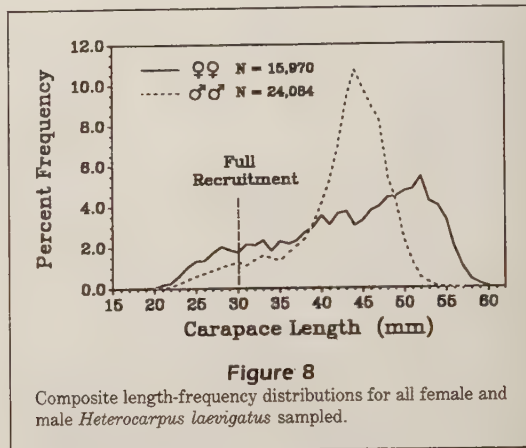


Figure 8

Composite length-frequency distributions for all female and male *Heterocarpus laevis* sampled.

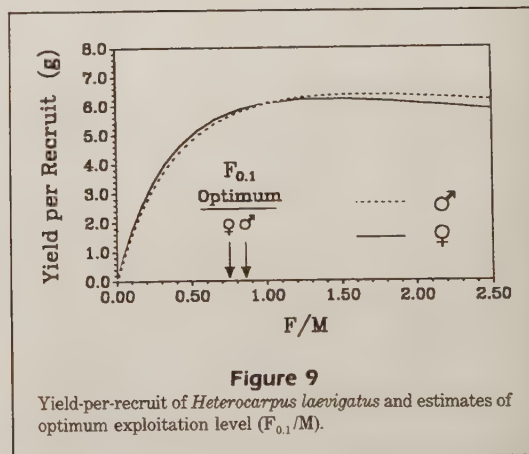


Figure 9

Yield-per-recruit of *Heterocarpus laevis* and estimates of optimum exploitation level ($F_{0.1}/M$).

The smallest shrimp we captured in the pyramid traps was 16 mm CL. Below this size, selectivity of the gear was zero. By equating carapace width and mesh size, we determined that $CL_{\infty} = 30$ mm. Thus, our estimate of the size at 50% recruitment to the fishery ($CL_{0.5}$) is 23 mm. Given this result, and sex-specific estimates of Θ and W_{∞} , we calculate that for females $F_{0.1}/M = 0.75$ and for males $F_{0.1}/M = 0.86$ (Fig. 9).

Discussion

In this assessment, projections of exploitable biomass depend greatly on the estimate of catchability obtained from the Leslie depletion experiment. Due to its major role in the calculations, sources of bias in its estimation must be considered carefully.

There is evidence to show that estimates of crustacean population size obtained through survey removal methods like the Leslie and DeLury methods (Ricker 1975) may severely misrepresent the actual size of the population. In his study, Morrissy (1975) found that DeLury estimates of population number of *Cherax tenuimanus* were anywhere from 39 to 53% of those based on a complete count of the population. Similarly, DeLury estimates of the population density of *Panulirus cygnus* were 25% of those estimated from diver counts (Morgan 1974a).

The most likely origin of bias in these situations is that not all individuals in the exploitable portion of the population are equally vulnerable (*sensu* Morrissy 1973) to the gear. For example, when sampling with baited drop nets, the catch of *C. tenuimanus* in intermolt, expressed as a known fraction of the actual population, was much higher than the catch in a premolt condition; individuals in molt stages immediately preceding and following ecdysis were not caught at all (Morrissy 1975).

It is possible that a similar bias was operating during the depletion study at the Kaulakahi Channel study site. The presence of shrimp in the exploitable portion of the population, which were less susceptible to trapping, would result in overestimation of catchability and underestimation of biomass. Factors such as molt stage (Morgan 1974b, Morrissy 1975), sex (Morrissy 1973), and feeding history (Sainte-Marie 1987) are known to cause variation in vulnerability to trapping. Although social dominance, mediated through differences in size, can affect catchability (Morrissy 1973, Chittleborough 1974), it is unlikely to have substantially biased our results because the catch size-structure remained unchanged during the experiment (Fig. 3). Also, Gooding et al. (1988) did not see "any overt aggressive behavior" among *H. ensifer* that were active around baits. Lastly, seasonal and interannual alterations in catchability due to temperature (Chittleborough 1970, Morgan 1974b), salinity (Morgan 1974b), and food availability (Chittleborough 1970) operate over longer time-scales than the depletion experiment.

Two other lines of evidence support the premise that shrimp biomass was underestimated. Although results presented in Figure 4 indicate that 12 days of trapping dropped the catch rate to 48% of its starting value (10.87 kg/trap-night), it had risen to 19.73 kg/trap-night when resampled 47 days later (data from 9–11 July 1986 cruise; see Table 1). If catchability is estimated from the decline in catch rate that occurred between the beginning of the depletion study (22.84 kg/trap-night) to the time the site was resampled 2 months later, and we assume the decline was due only to trap removals (1499.00 kg), we obtain $\hat{q} = 2.4624$ ha/trap-night. This represents a 74% reduction in the estimate,

which in turn would inflate biomass estimates by a factor of 3.85 (i.e., $B_{\Sigma\text{tot}} = 1050$ MT). This relative bias is similar to that reported by Morgan (1974a) for *Panulirus cygnus* (see above).

From submersible observations of *H. laevisgatus* density, Moffitt and Parrish (1992) obtained $\hat{q} = 0.2895$ ha/trap-night for the same traps we used, amounting to a 33-fold difference relative to our Leslie analysis. They, too, expressed concerns about bias in catchability estimates derived from depletion experiments due to variable susceptibility to the gear. Conversely, their estimate of catchability was based on comparing site-specific March 1988 trap catches with submersible observations made during August, even though *H. laevisgatus* undergoes seasonal vertical migrations (King 1983, Dailey and Ralston 1986). In addition, at the start of each dive, they deployed a baited trap in the area of the submersible. Both factors could lead to underestimation of catchability.

It is clear that biased estimates of q will result if the probability of capture is not uniform among shrimp. In an attempt to solve this problem, Quinn (1987) developed a depletion model that explicitly incorporated a term for non-constant catchability. Application of his model to Pacific halibut effectively accounted for short-term trends in q , but auxiliary estimates of fishing and natural mortality were required, data that are unavailable here.

The primary objective of this study was to determine the exploitable biomass of *H. laevisgatus* in the main Hawaiian Is. (MHI). Even if shrimp biomass were as high 1050 MT, rather than 271 MT (see above), our results indicate that the MHI stock is much smaller than previously believed, and that prior estimates of maximum sustainable yield (MSY) are much too high. For example, Struhsaker and Aasted (1974), using figures from a fishery for *H. reedi* off the coast of Chile, speculated that *H. ensifer* in Hawaii could sustain a level of production equal to 10–20 kg/ha $\cdot$ yr⁻¹. If *H. laevisgatus* were assumed to be equally productive (e.g., Anon. 1979), then, given there are $\sim 350,000$ ha of prime habitat at 458–640 m (250–350 fm) in the MHI alone (Table 2), the resulting estimate of MSY exceeds stock biomass many times over. Moreover, catch rates of *H. laevisgatus* in the distant Northwestern Hawaiian Is. (Nihoa to Kure), which represent a similar amount of shrimp habitat as the MHI, are no more than half those observed in the MHI (Gooding 1984, Tagami and Barrows 1988, Tagami and Ralston 1988).

Our estimates of $\Theta_\phi = 1.01$ and $\Theta_\sigma = 0.74$ are much lower than those given in Dailey and Ralston (1986), who reported $\Theta_\phi = 2.9$ and $\Theta_\sigma = 4.3$. By requiring CL_∞ to be greater than the modal size, they effectively constrained Θ to values much greater than unity. A similar requirement was imposed by Moffitt and Polovina

(1987), who estimated $\Theta_0 = 1.9$ and $\Theta_\sigma = 2.1$ for *H. laevis* in the Mariana Is. Additionally, use of the "mode" criterion to establish the minimum size at full vulnerability results in substantially greater sensitivity of Θ to input estimates of CL_{50} . For example, if CL_{50} is 30 mm as we suggest (Fig. 8), ± 2 mm perturbations in CL_{50} result in -9% and $+12\%$ changes in estimates of Θ_σ . However, if the mode of the size-frequency distribution is used instead ($CL_{50} = 44$ mm), the same perturbations alter estimates of Θ_σ by -16% and $+46\%$. Similar sensitivity was observed in estimates of Θ_0 . In summary, it is our belief that independent estimates of CL_{50} are superior to those obtained from the size data analyzed, particularly when there is no reason to suspect that agonistic interactions affect the catch size-structure.

Lower values of Θ indicate a reduction in the instantaneous mortality rate (Z), an increase in the von Bertalanffy growth coefficient (K), or both. We favor the first hypothesis, largely because of the cold ($4-6^\circ\text{C}$), trophically-impooverished habitat in which *H. laevis* reside. In many respects these shrimp represent a crustacean analog to Pacific ocean perch *Sebastes alutus*, which grow very slowly, exhibit extreme longevity, and display low rates of natural mortality (Leaman and Beamish 1984). Consequences of this life-history pattern are that (1) under pristine conditions, individuals accumulate in the largest size-categories (Fig. 8), (2) the ratio of production to biomass is low, and (3) stocks are very susceptible to overfishing.

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Abstract.—The diets of pelagic juveniles of widow rockfish *Sebastes entomelas*, yellowtail rockfish *S. flavidus*, chilipepper *S. goodei*, shortbelly rockfish *S. jordani*, and bocaccio *S. paucispinis* were compared using samples collected during 1984–87. All five species co-occur as pelagic juveniles off central California. Frequency of occurrence, percent by number, and a ranking index of prey items were determined from 1088 stomachs. Major prey of pelagic juvenile rockfish were the various life stages of calanoid copepods and subadult euphausiids (including eggs).

For each year, dietary overlap was quantified between interspecific pairs using the Colwell and Futuyma (1971) index. Amount of overlap varied from year to year. Long-term intraspecific dietary overlap, based on the 4 years of data, was generally less than interspecific overlap within years. Year-to-year variation in the diets of these species was generally greater than within-year variation among them, suggesting that, as a group, pelagic juvenile rockfishes are opportunistic feeders. Also, if interannual variation in the distribution and abundance of foods has a major impact on recruitment, the high dietary overlaps of these co-occurring species would suggest parallel survival and year-class success.

Multivariate analysis of variance was used to examine the effects of latitude, depth, and fish size on food consumption. Alterations in diet were related to latitude, depth, and a latitude-depth interaction for three species in 1987 and, also, for shortbelly rockfish in 1984–86. Diet was apparently unrelated to fish size.

Interannual variation and overlap in the diets of pelagic juvenile rockfish (Genus: *Sebastes*) off central California

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Rockfishes of the genus *Sebastes* are a major component of the west coast groundfish fishery (Gunderson and Sample 1980), yet little is known of their early life history. Kendall and Lenarz (1987) noted a particular lack of information on the biology of the pelagic juvenile life-stage. To date most work on pelagic juveniles has addressed problems in identification (e.g., Moser et al. 1977, Laroche and Richardson 1980 and 1981, Matarese et al. 1989), growth (Boehlert 1981a, Boehlert and Yoklavich 1983, Penney and Evans 1985, Laidig et al. 1991, Woodbury and Ralston 1991), and vertical distribution (Boehlert 1977 and 1981b, Moser and Alhstrom 1978, Moser and Boehlert 1991, Lenarz et al. 1991).

Female rockfishes undergo internal fertilization and the eggs develop within the ovary for a 40–50 day period (Kendall and Lenarz 1987). Larvae hatch internally, are extruded approximately 1 week later, and begin feeding. Larvae grow and transform into juveniles, a developmental stage characterized by the attainment of full meristic characters. Many rockfishes have a pelagic juvenile stage.

Pelagic juveniles ranging in size from 15–100 mm SL are abundant off central California from April to June, although distributional patterns vary markedly among species and years (Wyllie Echeverria et al. 1990). The pelagic juvenile stage ends with settlement into demersal or nearshore habitats.

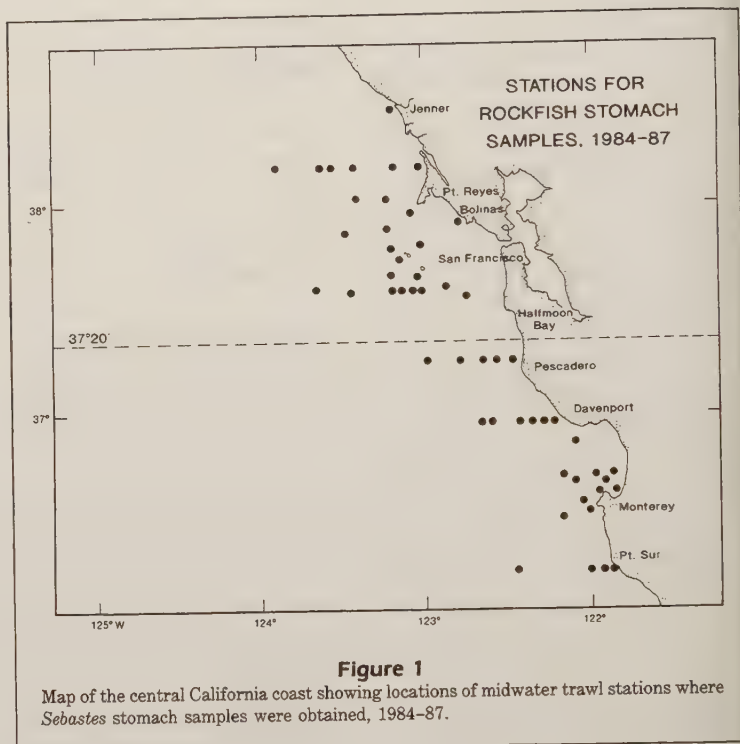
Evidence strongly indicates that the recruitment of marine fishes is heavily influenced by events that occur early in the life history (Blaxter 1974). A frequently proposed explanation is that the availability and abundance of foods appropriate for first-feeding larval and later juvenile stages are critical to adequate survival and growth. A reduction in the fine-scale density of suitable prey items, whether due to an absolute decrease in prey abundance (Hjort 1914) or to a randomized dispersion of what formerly was a patchy prey resource (Lasker 1975), can have a negative impact on survival. Reduced prey densities can affect survivorship directly through starvation, or indirectly by reducing growth rates and thereby prolonging exposure to other size-specific mortality factors

(e.g., predation, advection, etc.). Regardless of the mechanism, variation in the availability of food can have a major effect on year-class strength (Lasker 1981). The study of food utilization patterns and diet overlap is, therefore, useful in understanding survival mechanisms during the pelagic juvenile life stage. Moreover, annual variation in the extent of interspecific dietary overlap may indicate changes in the distribution and abundance of prey (e.g., Zaret and Rand 1971). Since this may well be critical in determining the success of a year-class, similarity in food habits among pelagic juvenile rockfish may result in similar recruitment dynamics.

Previous published dietary studies of juvenile rockfish have been limited to (1) experimental work on food ration and growth in black rockfish (*S. melanops*, Boehlert and Yoklavich 1983); (2) a description of the diet of newly settled Pacific ocean perch (*S. alutus*, Carlson and Haight 1976); (3) a comparison of the food habits of seven *Sebastes* spp. in a nearshore kelp-forest habitat (Singer 1985); and (4) predation on barnacle larvae by a mixed assemblage of settled kelp resident juvenile rockfishes (Gaines and Roughgarden 1987). The purpose of this study was to examine the feeding ecology of several co-occurring young-of-the-year pelagic juvenile rockfishes, including widow rockfish *S. entomelas*, yellowtail rockfish *S. flavidus*, chilipepper *S. goodei*, shortbelly rockfish *S. jordani*, and bocaccio *S. paucispinis*. Specific goals of this study were to (1) identify the food habits of these five species during the pelagic juvenile stage, (2) determine the extent of dietary overlap among the five species, and (3) determine the degree of interannual variation in patterns of prey utilization.

Materials and methods

Juvenile rockfish used in this study were obtained from midwater trawl samples made during a series of annual pelagic juvenile rockfish surveys conducted off central California during 1984–87. Details of these surveys are described in Wyllie Echeverria et al. (1990).



The primary purpose of the surveys was to estimate the distribution and abundance of the pelagic-stage juveniles of age-0 rockfishes. Survey areas and dates differed somewhat from year to year (Fig. 1, Table 1). The surveys were conducted during June, except in 1987 when the survey extended from late-May to June. In 1984 and 1985, the survey area extended from Point Sur (lat. 36°18'N) to Point Cabrillo (lat. 39°20'N). Bottom depths at each trawl station ranged from <50 m at nearshore localities to >3700 m beyond the continental shelf. The sampling plan was revised in 1986; seven transects composed of 36 stations were selected based on previous records of rockfish abundance and the availability of ship time. These stations were sampled repetitively during three consecutive sweeps of the area. After 1985, the survey area extended from Cypress Point (lat. 36°35'N) to Point Reyes (lat. 38°00'N), with station depths ranging from <50 to 1000 m.

Collections were made from the RV *David Starr Jordan* with a modified Cobb midwater trawl net having a 24.4 m head rope and 0.76 cm mesh liner in the cod-end. The standard depth sampled was 30 m. However, at shallow stations (bottom depth <100 m) the net was set at 5–10 m. At some deep stations samples were

Table 1

Number of juvenile *Sebastes* stomachs examined from juvenile rockfish surveys, 1984-87.

Year	Survey dates	Species	No. of stomachs	Range (mm SL)
1984	8-24 June	Widow rockfish	15	40-63
		Yellowtail rockfish	40	36-56
		Chilipepper	20	38-55
		Shortbelly rockfish	120	30-65
		Bocaccio	50	21-77
1985	5-30 June	Widow rockfish	75	43-63
		Yellowtail rockfish	30	39-48
		Shortbelly rockfish	85	49-75
1986	3-25 June	Yellowtail rockfish	10	35-47
		Shortbelly rockfish	168	15-47
		Bocaccio	25	18-40
1987	23 May-21 June	Widow rockfish	105	48-80
		Yellowtail rockfish	17	39-52
		Chilipepper	125	41-76
		Shortbelly rockfish	150	17-78
		Bocaccio	53	22-86
Total stomachs examined			1088	

A ranking index, modified from Hobson (1974), was calculated for the major food items. The index (I_r) is the product of proportional frequency of occurrence and percent by number, calculated for all specimens of a species in a year. To quantify dietary overlap among species, the index of Colwell and Futuyma (1971) was used, that is,

$$C_{ih} = 1.0 - 0.5 \left(\sum_{j=1}^n p_{ij} - p_{hj} \right),$$

where p_{ij} and p_{hi} are the numerical proportions of prey $j = 1 \dots N$ found in the diets of species i and h , respectively. The index has a minimum value of zero, when no overlap occurs, and a maximum value of one, when all prey are shared in equal proportions by the two species.

also collected at 100 m. Nets were fished for 15 min at depth during the night, ~30 min after sunset, or before sunrise.

Five specimens of each species were randomly subsampled from each haul for dietary analysis. Generally, no samples were taken if fewer than five individuals were taken in a haul. Specimens were tentatively identified to species and preserved whole in 10% buffered formalin, usually within 1 hour of collection. Identifications were later verified ashore with meristics keys (Matarese et al. 1989, Moreland and Reilly 1991); samples were transferred to 70% isopropyl alcohol within 1 month of collection. Standard length (SL) was later measured to the nearest 0.1 mm. Stomachs were removed and stored in 70% isopropyl alcohol until examined.

Stomach contents were examined with a dissecting microscope. Empty stomachs were noted and the digestive state of each prey item was coded on a scale of 1-3, with 3 representing digestion too advanced for identification. All prey types were identified to the lowest possible taxonomic level and counted. When possible, a subsample of all prey types was measured along the longest axis with an ocular micrometer. Heads or eyes were used to obtain total counts when food items were fragmented. For each rockfish species, the proportion of prey types in the diet was calculated as the percentage of total prey numbers consumed in a year, summed over all the individuals examined for stomach contents.

Multivariate analysis of variance (MANOVA) was used to examine relationships among latitude, bottom depth, and the diets of chilipepper, shortbelly, and widow rockfish (Green 1978, SAS 1985). Although only in 1987 were there sufficient data to analyze the diets of all three species, adequate samples of shortbelly rockfish were obtained during all years (1984-87). Thus, examination of overall variation in diet through time, vis-à-vis latitude and depth, was limited to shortbelly rockfish. Analyses were confined to the three prey types of highest frequency of occurrence during the year examined, which varied among the different species and years. The numerical proportions of the three prey types (the dependent variables) were arcsine-transformed (Sokal and Rohlf 1981) prior to MANOVA testing. Latitude, depth, and a latitude-depth interaction term were the independent variables. Station latitude was classified as either north or south of lat. 37°20'N. Similarly, station depth was divided into deep (>100 m) or shallow (<100 m) categories. Data for chilipepper, shortbelly, and widow rockfish sampled in 1987 were also divided into large (>1987 median SL) and small (<1987 median SL) size-classes to examine diet variation as a function of fish size. Shortbelly rockfish were sufficiently numerous during all years to analyze diet variation as a function of predator size. Prey types for this analysis were again limited to the three prey categories with the highest overall frequencies of occurrence in a year, and the dependent variables were the arcsine-transformed numerical proportions in the diet.

Table 2

Summary of stomach contents for five species of pelagic juvenile *Sebastes*, 1984. FO = frequency of occurrence; % = percent by number.

Prey category	Widow rockfish (n 15)		Yellowtail rockfish (n 40)		Chilipepper (n 20)		Shortbelly rockfish (n 120)		Bocaccio (n 50)	
	FO	%	FO	%	FO	%	FO	%	FO	%
EUPHAUSIACEA										
Furcilia	33.3	10.1	50.0	12.3	30.0	6.8	54.2	35.1	36.0	24.1
Calyptopis			2.5	0.3			1.0	0.1	2.0	0.2
Juveniles	20.0	3.2	15.0	3.4	15.0	2.6	14.1	10.2	38.0	25.3
AMPHIPODA										
Hyperiid juveniles							1.0	0.1	4.0	0.3
CUMACEA							1.7	0.1		
DECAPODA										
Natantia juveniles	6.7	0.5					1.0	0.2		
COPEPODA										
<i>Calanus</i> spp.	46.7	41.0	52.5	28.7	40.0	27.2	40.8	15.1	34.0	31.6
<i>Candacia</i> sp.			5.0	0.4			6.7	0.5	2.0	0.2
Copepods (unidentified)	26.7	17.6	47.5	14.7	15.0	10.5	36.7	12.0	30.0	15.8
Juveniles	20.0	27.7	17.5	40.2	40.0	52.9	10.8	26.8	2.0	0.9
OSTEICHTHYES										
Fish larvae (unidentified)									20.0	1.7

Results

Frequency of occurrence and percent number

Stomachs from 1088 pelagic juvenile rockfish collected from midwater trawls during the four survey years (Table 1) were examined. Frequency of occurrence and percent number for specific prey types of each rockfish species varied considerably from year to year (Tables 2–5). In 1984, bocaccio differed from all other rockfish species in the frequency of occurrence of fish larvae as a prey type (Table 2). Euphausiid eggs occurred in the stomachs of all three species in 1985, although there is a disparity in the percent number (Table 3). Euphausiid eggs were much less frequent in the diets of the three rockfish species in 1986 (Table 4), whereas juvenile euphausiids occurred more frequently. Overall, data from 1984–87 show that prey items having a high frequency of occurrence generally had a high percentage by number. Euphausiid eggs and juveniles and unidentified copepods often had high percentages by number relative to their frequencies of

Table 3

Summary of stomach contents for three species of pelagic juvenile *Sebastes*, 1985. FO = frequency of occurrence; % = percent by number.

Prey category	Widow rockfish (n 75)		Yellowtail rockfish (n 30)		Shortbelly rockfish (n 85)	
	FO	%	FO	%	FO	%
EUPHAUSIACEA						
Furcilia	22.7	1.7	30.0	1.2	14.1	0.4
Calyptopis	2.7	0.1	6.7	1.5	1.2	0.1
Juveniles	5.3	0.7	10.0	0.2	16.5	0.4
Euphausiid eggs	18.7	8.2	36.7	59.1	48.2	59.3
AMPHIPODA						
Hyperiid juveniles	6.7	0.1	3.3	0.1	7.1	0.1
LARVACEA	6.7	4.1			7.1	2.4
CHAETOGNATHA	1.3	0.1				
DECAPODA						
Natantia juveniles			3.3	0.1	1.2	0.1
COPEPODA						
<i>Calanus</i> spp.	22.7	1.7	16.7	1.2	25.9	1.2
<i>Candacia</i> sp.	2.7	0.1	3.3	0.1	1.2	0.1
Copepods (unidentified)	13.3	3.7			17.6	2.9
<i>Eucalanus</i> sp.	8.0	1.8			3.5	0.1
<i>Euchirella</i> sp.	2.7	0.2			3.5	0.1
Juveniles	44.0	77.6	56.7	36.5	57.6	33.3
<i>Metridia</i> sp.			3.3	0.1	1.2	0.1
OSTEICHTHYES						
Fish larvae (unidentified)	1.3	0.1				

Table 4

Summary of stomach contents for three species of pelagic juvenile *Sebastes*, 1986. FO = frequency of occurrence; % = percent by number.

Prey category	Yellowtail rockfish (n 10)		Shortbelly rockfish (n 168)		Bocaccio (n 25)	
	FO	%	FO	%	FO	%
EUPHAUSIACEA						
Furcilia	10.0	1.6	13.2	0.9	4.0	0.2
Calyptopis	10.0	0.6	3.6	0.1		
Juveniles	70.0	7.1	59.9	10.0	52.0	22.0
Euphausiid eggs			4.8	1.1		
CUMACEA	10.0	1.0	1.2	0.1		
DECAPODA						
Natantia juveniles	20.0	1.0	0.6	0.1		
COPEPODA						
<i>Calanus</i> spp.			38.3	6.6	64.0	30.5
Copepods (unidentified)			34.1	3.9	28.0	5.9
<i>Epilabidocera</i> sp.	40.0	8.7				
Juveniles	50.0	80.1	71.9	77.3	44.0	41.4

occurrence. Euphausiid eggs and juvenile copepods were the smallest significant prey of pelagic juvenile rockfish. It is therefore not surprising that these categories often display high percentages by number. Likewise, the category 'unidentified copepods' typically was based on counts of small items (e.g., head fragments).

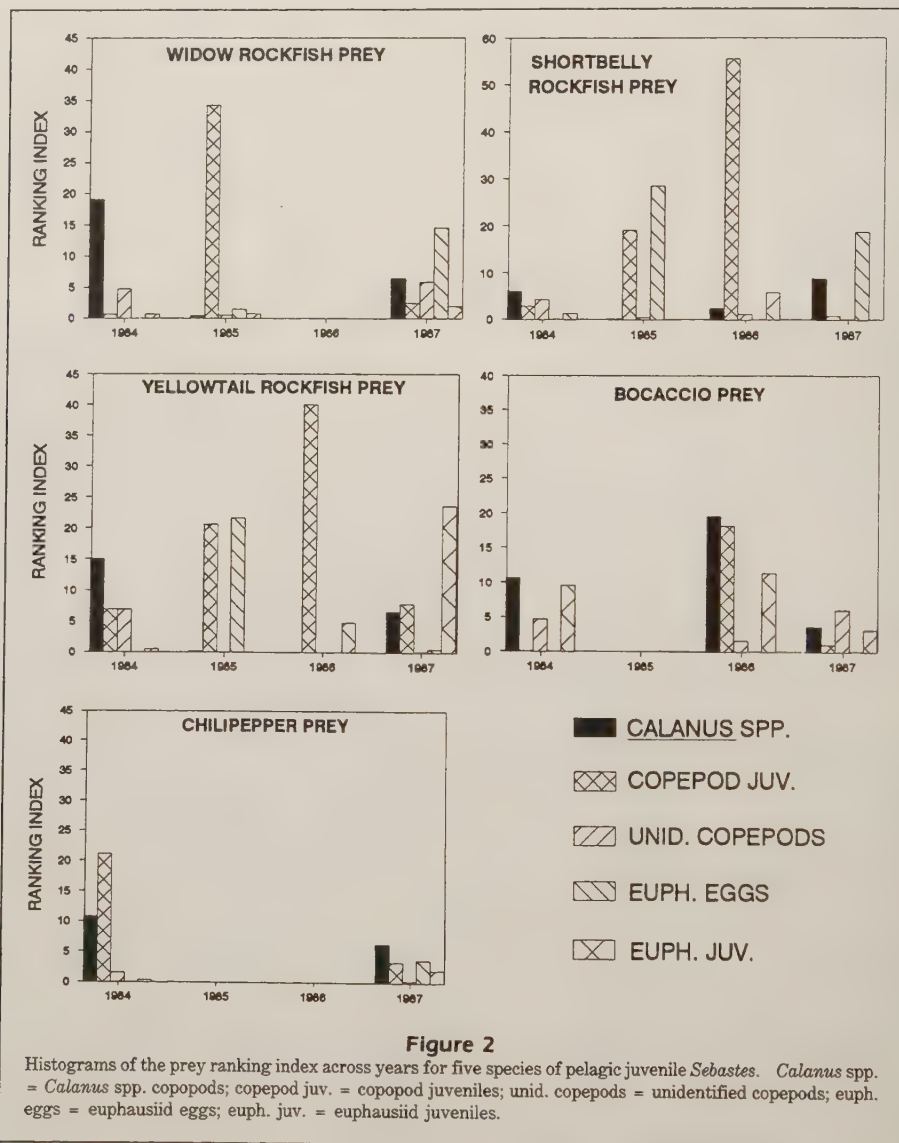
Ranking index

Prey having both a high frequency of occurrence and percentage by number are the most important items in the diet (Tables 2-5). *Calanus* spp. copepods were particularly important in 1984 when all rockfish species consumed substantial numbers of this

Table 5

Summary of stomach contents for five species of pelagic juvenile *Sebastes*, 1987. FO = frequency of occurrence; % = percent by number.

Prey category	Widow rockfish (n 105)		Yellowtail rockfish (n 17)		Chilipepper (n 125)		Shortbelly rockfish (n 150)		Bocaccio (n 53)	
	FO	%	FO	%	FO	%	FO	%	FO	%
EUPHAUSIACEA										
Furcilia	6.6	0.20	11.8	1.1	8.0	1.30	40.7	4.00	1.9	0.1
Calyptopis	8.5	0.30	5.9	0.4	2.4	0.40	6.7	1.60	1.9	0.1
Juveniles	39.6	9.00	76.5	31.1	19.8	10.30	6.7	0.60	30.2	10.7
Euphausiid eggs	27.4	52.00	5.9	7.7	10.4	35.80	28.7	65.80	1.9	10.5
Euphausiids (unidentified)	8.5	0.30	5.9	0.2	8.0	0.60	8.0	0.20		
<i>Euphausia</i> sp.									3.8	0.2
<i>Thysanoessa</i> sp.	1.0	0.01								
AMPHIPODA										
Hyperids	1.0	0.01			1.6	0.10	1.0	0.01	1.9	0.1
CUMACEA					1.0	0.04				
DECAPODA										
Natantia juveniles	1.0	0.04			1.0	0.04				
Crab megalopa					3.2	0.20				
Crab zoea					1.6	0.10	1.0	0.01		
CIRRIPEDIA										
Cypris larva							1.0	0.10		
COPEPODA										
<i>Calanus</i> spp.	33.0	19.80	47.1	13.9	28.0	22.80	44.0	20.30	32.1	11.5
<i>Candacia</i> sp.					1.0	0.10			1.9	0.2
Copepods (unidentified)	22.6	7.30	5.9	1.1	8.0	4.10	4.0	1.00	13.2	45.8
<i>Eucalanus</i> sp.	1.9	0.10							1.9	0.1
<i>Euchaeta</i> sp.									1.9	0.8
<i>Rhincalanus</i> sp.	1.0	0.01					1.0	0.01		
Juveniles	24.5	10.00	17.7	44.5	14.4	24.30	16.0	6.30	5.7	19.3
TEUTHOIDEA										
Squid larva									1.9	0.1
OSTEICHTHYES										
Fish larvae									15.1	0.6
Eggs	3.8	1.00					2.0	0.40		



prey. Likewise, 1985 was a year in which copepod juveniles and euphausiid eggs dominated the diets of the three species examined (widow, yellowtail, and shortbelly rockfish) and copepod juveniles were again important to all species in 1986.

Interspecific prey utilization patterns were less obvious. There is some indication that widow and chilipepper rockfish consumed more copepod juveniles and *Calanus* spp. copepods than did the other species.

Similarly, shortbelly rockfish appeared to consume more euphausiid eggs, while bocaccio consumed more euphausiid juveniles. Likewise, there was some suggestion that bocaccio fed on larger prey than the other species (e.g., euphausiid adults and fish larvae). Nonetheless, no distinctive separation in primary prey species was evident among the five species examined.

Based on the I_r ranking index, it is apparent that the diet of pelagic juveniles is typically dominated by

a single prey type each year, followed by several prey types with indices at much lower values (Fig. 2). There were few instances in which the two most important prey types were similar in ranking index, e.g., yellowtail rockfish consuming euphausiid eggs (21.7) and juvenile copepods (20.7) in 1985. This result suggests that each year these species, to a large extent, specialize on foods that are intermittently abundant. Also, the ranking index data, together with information on frequency of occurrence and percent by number, indicate the major prey items of pelagic juvenile rockfish were various life stages of copepods and subadult euphausiids.

Dietary overlap

The extent of interspecific dietary similarity was quantified by comparing dietary overlaps among all possible pairs of species within each year (1984–87). Ten species pairs were possible, but not all pairs were observed each year since all five species were not always collected (Table 6). Overlap indices are sensitive to the taxonomic level to which prey items are categorized; thus, statistical tests of significance concerning the data are arbitrary. Therefore, the convention established by Langton (1982) and Brodeur and Pearcy (1984) was invoked. Overlap index values of 0.00–0.29 were considered low, values of 0.30–0.60 were considered medium, and values >0.60 were considered high.

Using these criteria, annual comparisons of the distribution of overlap indices for 1984 indicate that 60% of all comparisons were classified as medium and 40% were classified as high. Results from 1985 and 1986 indicate that 67% of the scores were medium and 33% were high. In contrast, index values during 1987 generally had the lowest amount of overlap: 10% low, 70% medium, and 20% high. Based on these findings we conclude that, although overall patterns of dietary overlap do vary from one year to the next, variations are relatively modest (only in 1987 was any low overlap observed). Moreover, in this study most within-year species pairings showed >30% overlap. The principal exception to this generalization was for yellowtail and shortbelly rockfish sampled in 1987. Their diets were quite dissimilar.

Overlap indices were also calculated for all possible interannual intraspecific combinations. These calculations allow an assessment of the temporal stability of the diet relative to the amount of interspecific dietary overlap displayed during a given year. The frequency distribution of dietary overlap values derived from self-pairing of rockfish species from different years is shifted well to the left (toward zero) of the distribution of interspecific scores obtained within a year (Fig. 3). These findings show that in any particular year the dif-

Table 6
Diet overlap indices for individual pairings of pelagic juvenile *Sebastes* (1984–87). Wid = widow rockfish; Yel = yellowtail rockfish; Chi = chilipepper; Sho = shortbelly rockfish; Boc = bocaccio.

Species pair	Year			
	1984	1985	1986	1987
Wid-Yel	0.84	0.53	—	0.39
Wid-Chi	0.58	—	—	0.69
Wid-Sho	0.52	0.46	—	0.77
Wid-Boc	0.57	—	—	0.50
Yel-Chi	0.61	—	—	0.52
Yel-Sho	0.58	0.90	0.91	0.22
Yel-Boc	0.64	—	0.46	0.48
Chi-Sho	0.38	—	—	0.56
Chi-Boc	0.41	—	—	0.49
Sho-Boc	0.61	—	0.51	0.30

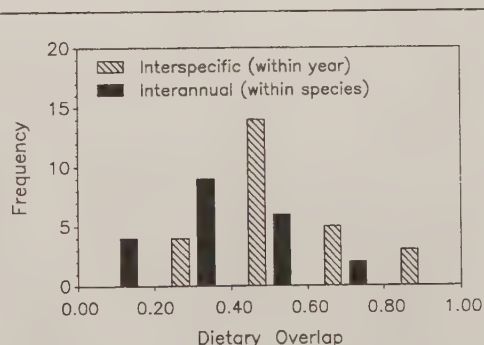


Figure 3

Frequency of dietary overlap indices among all interspecific *Sebastes* pairs within years, compared with frequency of overlap indices calculated for each *Sebastes* species self-paired across years.

ferent species of rockfish are opportunistic feeders that utilize relatively similar prey items, but substantial dietary change can occur from year to year.

Latitude and depth effects

Dietary variation with respect to station latitude (north or south of lat. 37°20'N), station depth (deeper or shallower than 100m), and the interaction of these variables were analyzed using MANOVA (Table 7). The statistical significance of each analysis depended on the particular combination of species and year examined. In 1987, highly significant ($P < 0.001$) diet variations occurred with depth for shortbelly and widow rockfish.

Table 7

Results of MANOVA of depth, latitude, and depth by latitude effects on three principal prey types of pelagic juvenile *Sebastes*. Cal = *Calanus* spp.; CoJv = copepod juveniles; EJv = euphausiid juveniles; EuEg = euphausiid eggs; ELv = euphausiid larvae; UnCo = unidentified copepods; Fur = furcilia.

Species	Year	Prey type			MANOVA model effects					
					Depth		Latitude		Depth * latitude	
		I	II	III	Wilks' λ	P	Wilks' λ	P	Wilks' λ	P
Chilipepper	87	Cal	CoJv	EJv	0.9019	0.0580 ^b	0.9186	0.1044	0.9715	0.5525
Widow	87	Cal	EuEg	EJv	0.6638	0.0001**	0.9536	0.2813	0.9805	0.6632
Shortbelly	87	Cal	EuEg	ELv	0.7649	0.0001**	0.9805	0.5059	0.9243	0.0252*
Shortbelly	86	Cal	CoJv	EJv	0.8917	0.0005**	0.7522	0.0001**	0.9404	0.0234*
Shortbelly	85	Cal	EuEg	CoJv	0.8934	0.0472*	0.9293	0.1600	0.9185	0.1121
Shortbelly	84	Cal	UnCo	Fur	0.9647	0.3110	0.9213	0.0429*	0.9095	0.0240*

Significance levels:

^bborderline

* $P < 0.05$

** $P < 0.01$

In that year, latitude had no discernible influence on the diet of these two species, although for shortbelly rockfish a significant interaction between depth and latitude was evident. These findings strongly suggest that spatial variability in the environment (i.e., latitude and depth of the water column) can influence, to some extent, the diets of pelagic juvenile rockfish in a species-specific manner.

Results for the full time-series of shortbelly rockfish data (1984–87) also show that spatial patterns change over time. Although depth had a highly significant effect on diet in 1986 and 1987, it was not significant in 1984 or 1985. Similarly, latitude had no appreciable relationship to the diet of shortbelly rockfish in 1985 and 1987, but it had a highly significant effect in 1986. Importantly, whenever a latitude correlation with diet was present, the interaction term (depth * latitude) was significant as well. We believe that the erratic influence of spatial structure on the shortbelly diet is likely due to the dynamic nature of the nearshore pelagic/neritic physical environment.

Using the 1987 data, we examined the least-squares means (Searle et al. 1980) of the transformed numerical proportions of the individual prey types to learn exactly how dietary composition varied when statistically-significant model effects occurred. In that year, the diet of chilipepper showed borderline significance with depth ($P = 0.058$); the least-squares means revealed that chilipepper consumed more *Calanus* spp. copepods in shallow water, and more juvenile copepods and juvenile euphausiids at bottom depths >100 m. Likewise, all three prey types (*Calanus* spp., euphausiid eggs, and juvenile euphausiids) of widow rockfish were consumed in greater proportion in deep water, especially euphausiid eggs.

For shortbelly rockfish, which displayed a significant interaction term, consumption of *Calanus* spp. copepods was noticeably depressed at shallow southern stations. Euphausiid eggs were consumed in much greater quantities at deep stations, both north and south, while fewer larval euphausiids (furcilia and calyptopis) were found in fish from northern deep stations.

Predator size

Results were inconsistent when these same data (i.e., numerical proportions in the diet of the three most frequently occurring prey items for 1984–87 shortbelly rockfish, 1987 chilipepper, and 1987 widow rockfish) were also explored with MANOVA to assess the effect of fish size on composition of the diet. In each instance, fish were assigned to either small or large size-classes, based on whether standard lengths were smaller or larger than the annual median of that species.

Of the six cases examined (Table 8) two yielded significant ($P < 0.05$) results. Large shortbelly rockfish sampled in 1986 tended to eat a higher proportion of *Calanus* spp. copepods, whereas small fish had a higher fraction of juvenile euphausiids and juvenile copepods in their diet. Results from that year, therefore, support the view that large fish tend to consume large prey. Even so, a significant size effect was demonstrated for 1985 shortbelly rockfish, which was exactly the opposite of 1986; large fish consumed fewer *Calanus* spp. copepods and a greater percentage of euphausiid eggs than did small fish. Sample size was not adequate to statistically analyze fish length jointly with distributional patterns. However, in 1985, 34 of

Table 8

Results of MANOVA of fish size on three principal prey types of pelagic juvenile *Sebastes*. Cal = *Calanus* spp.; CoJv = copepod juveniles; EJv = euphausiid juveniles; EuEg = euphausiid eggs; ELv = euphausiid larvae; UnCo = unidentified copepods; Fur = furcilia.

Species	Year	Prey type			Fish size	
		I	II	III	Wilks' λ	P
Chilipepper	87	Cal	CoJv	EJv	0.9927	0.9088
Widow	87	Cal	EuEg	EJv	0.9678	0.4407
Shortbelly	87	Cal	EuEg	ELv	0.9634	0.2132
Shortbelly	86	Cal	CoJv	EJv	0.9362	0.0161*
Shortbelly	85	Cal	EuEg	CoJv	0.8801	0.0261*
Shortbelly	84	Cal	UnCo	Fur	0.9928	0.8654

* $P < 0.05$

the 42 shortbelly rockfish that were classified as small came from deep stations. Results presented earlier (Table 7) showed that the diet of shortbelly rockfish varied significantly with depth in 1985 (i.e., fewer euphausiid eggs and copepod juveniles at deep stations). Thus, the conclusion that small fish consumed large prey in 1985 is, to some degree, confounded with this spatial effect.

Discussion

The five species of pelagic juvenile rockfish examined in this study consumed pelagic zooplankton almost exclusively. Relatively few prey types made up the major portion of the diet each year. Various life history stages of calanoid copepods and euphausiids dominated. Carlson and Haight (1976) reported that copepods and euphausiids were important in the diet of pelagic juvenile Pacific ocean perch *S. alutus*. Singer (1985) recently reported that settled juveniles of several rockfish species consumed copepods and zoea larvae in a central California kelp forest. Other studies (Robb and Hislop 1980, Bowman 1981, Conway 1980) have also demonstrated that calanoid copepods and euphausiids are extremely important foods to pelagic juvenile fishes in the northeastern Pacific Ocean. These studies demonstrate that the diets of pelagic juvenile rockfishes are similar to those of other species possessing pelagic juvenile life stages.

A significant finding of this study is that *Sebastes* spp. juveniles periodically forage heavily on euphausiid eggs. Euphausiid eggs have not been previously reported as a prey item of pelagic juvenile rockfish and yet they were a very important dietary component both in 1985 and 1987. During those years, euphausiid eggs

averaged over 37% of the prey items consumed by the five species studied. However, euphausiid eggs were absent from samples collected in 1984 and were a minor component in 1986.

Some species of euphausiids brood their eggs prior to hatching (e.g., *Nyctiphanes* spp.), whereas other species release eggs upon fertilization (e.g., *Euphausia pacifica* and *Thysanoessa spinifera*). Since adult euphausiids were not found in any stomachs in 1985 (Table 3), and since only the latter genera were encountered in large swarms in the study area in 1987 (Smith and Adams 1988), rockfish must have consumed eggs after release. It was not expected that a non-motile prey would constitute such an

important food resource to pelagic juvenile rockfish. The appearance of eggs in clumped masses in guts suggests that eggs were not individually picked from the plankton.

Another interesting finding was the consumption of fish larvae by bocaccio juveniles. A total 15–20% of all bocaccio sampled in 1984 and 1987 contained larval fish. In our surveys, bocaccio grow faster and reach larger sizes as pelagic juveniles (≥ 100 mm SL) than do other species (Woodbury and Ralston 1991). They are also distributed at shallower depths (Lenarz et al. 1991).

We used the I_j statistic to rank the importance of individual prey items in the diet. This statistic differs from a similar statistic used by Hobson (1974) in that it is the product of proportional frequency of occurrence and percent by number, rather than percent by volume. Use of this statistic allowed us to characterize the prey types consumed by *Sebastes* in each of the 4 years studied. No obvious species-specific patterns emerged in the absence of a temporal component.

Our results indicate that pelagic juvenile *Sebastes* tend to respond similarly to environmental fluctuations in their food base, suggesting an opportunistic feeding strategy. Intraspecific dietary overlap between interannual pairings was much lower than were interspecific interannual pairings. On a relative basis, interannual differences in diet were tracked similarly among the five species we examined. Annual changes in diet are likely to reflect annual differences in the composition, availability, and abundance of prey.

It was not possible to infer from our results whether or not food is limiting to pelagic juvenile rockfishes, given the relatively large interannual variation in the diet among these species and the likelihood that variation in the availability of prey is likely responsible.

Even so, high dietary overlap observed among co-occurring pelagic juvenile rockfishes suggests that similar recruitment dynamics must exist if the distribution and abundance of foods has a major impact on recruitment.

Intraspecific spatial variation was observed (Table 7), even though substantial interspecific overlap exists in patterns of food utilization. In some instances, parallel spatial differences were observed for different species. For example, in 1987 both widow and shortbelly rockfish fed on euphausiid eggs to a much greater extent in deep water (>100 m) than in shallow water. In other cases, however, species-specific differences in diet due to depth were reversed. In 1987, for example, the consumption of *Calanus* spp. copepods by chilipepper was higher in shallow water, while consumption by widow rockfish was higher in deep water.

With the exception of the predator-size MANOVA discussed previously (i.e., shortbelly rockfish in 1985), sample sizes for each treatment combination in all MANOVA tests were reasonably well balanced. Therefore, it is unlikely that our conclusions were compromised by our choice of statistical tests.

The spatial incongruity of within-year dietary patterns among species also extended to interannual within-species comparisons. For example, shortbelly rockfish sampled in 1984 and 1987 consumed substantially fewer *Calanus* spp. copepods in the shallow southern quadrant than anywhere else. However, in 1986 consumption of this prey was greatest in fish taken in this region.

These interspecific (within-year) and interannual (within-species) comparisons demonstrate a lack of stability in the specifics of how spatial dietary effects are expressed. It is likely that the complex nearshore pattern of circulation that characterizes the study area (frontal structures, mesoscale eddies, turbulent jets, and upwelling plumes are common recurrent features; Mooers and Robinson 1984, Flament et al. 1985, Njoku et al. 1985, Schwing et al. 1990) defines the spatial distribution of the zooplanktonic animals upon which these rockfish feed. Thus, the dynamic nature of the physical environment off central California generates spatial instabilities in the distribution and abundance of prey.

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POPULATION BIOLOGY AND STATUS OF EASTERN PACIFIC GRAY WHALES: RECENT DEVELOPMENTS

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Abstract. Gray whales (*Eschrichtius robustus*) of the eastern Pacific stock are perhaps the best-known population of baleen whales, but uncertainties remain concerning many aspects of their population biology. The most recent abundance estimate (1987/88) of 21 113 (SE 688) may be the most accurate and precise available for any baleen whale population; but the estimated confidence interval is problematic, most likely not reflecting all relevant sources of error. The population is estimated to have increased at an annual rate of 3.2% (SE 0.5%) during the 20-yr period 1967/68 to 1987/78, during which annual harvests of about 174 whales were taken by the Soviet aboriginal fishery. Data from this fishery indicate a steep decline in pregnancy rates during 1987 to 1990, from a relatively stable level during the preceding 20 yr. Three approaches have been used to determine the status of this population: back-calculation, dynamic response, and Bayesian estimation of parameters for a simple population dynamics model. None of these approaches produced unequivocal results, but the back-calculation produced reasonable trajectories of abundance through time with either a tripling of carrying capacity since 1846 or a 50% minimum increase in recorded catches. All uncertainty considered, the population is probably above its 1846 level, when commercial exploitation began, and may now be approaching current carrying capacity. The combination of net productivity exceeding 4% and indications that the population is nearing carrying capacity are consistent with the hypothesis that for most large mammals, maximum net productivity occurs at high population levels.

INTRODUCTION

Gray whales (*Eschrichtius robustus*) are perhaps the world's best studied baleen whales. Their abundance, distribution, behavior, life history, and ecology have been the subjects of numerous investigations. There are, however, important aspects in all these topics that are still poorly understood or controversial. In this paper I review progress during the past 7-8 yr resulting from efforts to understand their population biology, with

emphasis on information relevant to determining their present status. As discussed below, it is not entirely clear what should be used as a standard to evaluate present status.

Two distinct populations of gray whales are recognized, the western Pacific and eastern Pacific stocks. This review is concerned only with the eastern Pacific stock. The western Pacific stock, with very few surviving individuals, is clearly endangered (Klinowska 1991, Braham and Donovan 1992), but may have never numbered more than a few thousand. (Two Atlantic stocks are now extinct.) In April 1990 the International Whaling Commission (IWC) convened a meeting to conduct a "comprehensive assessment" of the status of gray whales (IWC 1990). I have drawn heavily from the papers and proceedings of that meeting in this review. Three major topics are covered: abundance and trends, biological parameters, and quantitative attempts to determine status.

ABUNDANCE AND TRENDS

There have been many field programs to estimate gray whale abundance, as reviewed by Reilly (1984b) for efforts up to 1980, and by Dahlheim and Rugh (1990) for subsequent efforts. There are three types of survey data: aerial surveys of the winter range in Mexican waters, shore-based sighting surveys along the coast of upper California during the north and south migrations, and aerial or ship surveys on the summer range in the Bering and Chukchi Seas. Of these surveys, only one is sufficiently reliable for estimation of abundance and trends in abundance. This is the annual survey of the south migration conducted since 1967/68 from points near Monterey, California. The other efforts were incomplete, covered variable parts of the population, and lacked sufficient corroborative data to allow reliable estimates of relative or absolute abundance (Reilly 1984b). Two counts from a coastal point of northbound migrants have shown promise for estimating annual calf production (Poole 1984) but these counts have not been made in recent years.

Sixteen annual surveys were conducted near Monterey during the 21-yr period ending in the winter of 1987/88 (Reilly et al. 1983, Breiwick et al. 1988). To make these counts, one or two observers viewed migrating whales from a bluff-top position 21 m above the water. Migrating groups or "pods" were in view for about one-half hour. As the pods passed the counting station, the observers recorded estimates of the number of individuals in the pod and their distance offshore, along with information on sighting conditions. This protocol was followed during all daylight hours, sampling about 10 of 24 h each day (Dahlheim and Rugh 1990).

Estimating abundance from the recorded counts involves correcting for: (1) pods missed entirely in the nearshore area, (2) pods missed due to their distance offshore, (3) pods missed due to poor visibility conditions, (4) those passing during unmonitored periods at night, (5) others missed before and after the census period, and (6) miscounting of individuals within sighted pods (Reilly 1984b, Breiwick et al. 1988).

In analyzing the first 13 years' data, Reilly et al. (1983) applied the following solutions to the six problems listed above. Only counts from days with "good or better" sighting conditions (Beaufort 4 or lower) were used. A gamma probability density function (PDF) was fit to each year's daily sighting data. Migration rates were estimated

from this PDF for days with poor visibility and for days before the beginning and after the end of the survey. Whales passing at night were estimated by a simple proportionality constant, assuming no difference between day and night migration rates. Aerial surveys indicated that about 20% of passing pods were missed as a function of their distance offshore. Experiments indicated consistent negative biases in counting numbers within sighted pods, and appropriate corrections were applied. Abundance estimates ranged from a low of 10 414 for 1971/72 to a high of 17 577 for 1979/80, with coefficients of variation (CV) of about 11%. The population exhibited a significant annual increase of 2.5% during 1967/68-1979/80, concurrent with an annual harvest of about 1.2% in the Soviet aboriginal fishery.

Three additional surveys were conducted, in the winters of 1984/85, 1985/86 and 1987/88 (Breiwick et al. 1988). Data from the 1984/85 and 1985/86 surveys suggested a different distribution of pods migrating offshore from the survey site compared to those of the previous 13 yr. To check this, the aerial surveys of 1978/79 and 1979/80 were replicated in 1987/88 (Withrow 1990). The aerial data were very similar to those collected earlier, but the 1987/88 shore count distribution was farther offshore than in the pre-1981 efforts. The 1987/88 shore and aerial distributions were not statistically different, indicating that the shore observers did not consistently miss whales as a function of their distance offshore that year. The discrepancy between the shore-based distributions from the early years and the more recent 3 yr is a problem, especially in attempts to measure trends over the entire 21 yr period (discussed below).

Rugh et al. (*in press*) tested the assumption of Reilly et al. (1983) that essentially all passing pods were seen within 1.5 nautical miles (2.7 km) of the shore during periods of unhampered visibility, by running two independent, parallel counting operations during the 1987/88 migration. They used mark-recapture methods to estimate that about 26% of passing whales were missed by the shore counts, even during periods of good visibility and within 10.5 nautical miles. Swartz et al. (1987) radio tagged 12 gray whales during the south migration past central California, and found that night and day migration rates were not different, supporting the assumption used earlier in abundance estimation.

Other differences in treating the recent 3 yr counts included the fit of Hermite Polynomial models to the migratory timing data (rate of pods passing per hour) instead of gamma models. These models were used to predict migration rates during all unmonitored periods, including nights, daylight hours with poor visibility, and the "tails" of the migration. This was done by integrating the area under the fitted model, and comparing this sum to the totals from the observed periods. The ratio of these sums was used as an estimate of the proportion of pods missed during unmonitored periods. The recorded number of pods was then scaled up by this ratio estimate. Breiwick et al. (1988) also assumed the actual number of pods counted to be subject to variability that was greater than that of a poisson distribution by a factor estimated from the fit of the Hermite Polynomial, and estimated a SE for this factor. The corrections applied and their SE are listed in Table 1 for the 1987/88 absolute abundance estimate of 21 113.

This abundance estimate is perhaps the most accurate of any for a large whale population. In comparison to ship or aerial surveys of pelagic species, or breeding/feeding area counts of dispersed populations of humpback and right whales, a relatively large proportion of the gray whale population is actually observed. This is made possible by the mild winter climate at the survey site, and the migration of the vast

majority of the population past Monterey, very close to shore. The problems of estimating total abundance from recorded shore counts have been addressed for decades, with many refinements achieved (Rice and Wolman 1971, Reilly et al. 1983, Reilly 1984b, Breiwick et al. 1988, Buckland 1990).

I am not so confident in the magnitude of the 1987/88 abundance estimate's SE. In particular, the SE for the Hermite Polynomial model's correction factor for unmonitored periods is suspiciously small with a CV of 0.003 for that correction. This implies that it is possible to estimate the number of pods passing during over 60% of the migration to within less than 1% of the true number with 95% confidence, given the observed rates during the other 40% of the migration. In my opinion, the process of variance estimation for the 1987/88 abundance estimate, and subsequent application of this process to the rest of the time series, requires some reevaluation. Examination of Fig. 1 provides empirical evidence that the SEs estimated as in Breiwick et al. (1988) are too small. The 95% confidence limits of adjacent years do not overlap in four cases. This disparity is most extreme for 1971/72 versus 1972/73. Although the specific variance components that have been quantified may be technically correct, there are clearly other, unquantified components of variance. S. T. Buckland (*personal communication*) suggested that these SE estimates might be considered as lower bounds, and that upper bounds could be obtained from the mean residual of the annual estimates in Fig. 1 from the fitted, exponential line.

TABLE 1. Corrections applied, their standard errors (SE) and coefficients of variation (CV) for the 1987/88 estimate of gray whale abundance, from Breiwick et al. (1990).

Parameter	Estimate	SE	CV
pods seen	2902	81.1	0.028
unmonitored time	20.574	0.009	0.003
mark-recapture	1.260	0.014	0.011
pod size + bias cf	2.243	0.027	0.012
Abundance	21 113	688	0.033

Buckland (1990) also had to contend with the apparent inconsistencies in offshore distribution from the pre- and post-1981 shore surveys in his estimation of trend over the entire 21-yr period. Because the distributions from aerial surveys prior to 1981 showed no substantial differences from that collected after 1981, Buckland (1990) believed that the most likely explanation for the differences in the shore data was a consistently large negative bias in distance estimation by land-based observers during the first 13 yr. In support he cites the use in post-1981 surveys of binoculars with reticles (etched lines in

the lenses corresponding to known angles and therefore estimable distance categories). Lacking a satisfactory method to correct for this explicitly, he assumed there were no interannual trends in bias in detecting pods with distance, or in the true proportion of whales passing out of sight from land.

Buckland (1990) estimated relative abundance for years prior to 1987/88 by scaling up recorded counts with the Hermite Polynomial correction factor (for unmonitored periods) and multiplying by the average pod size. For 1987/88 an estimate of absolute abundance was made by further applying the correction factors for pod size bias, and for pods missed entirely (from the mark-recapture estimate). The other years were then scaled up for trend estimation by the ratio of the relative to absolute estimates for 1987/88. A regression of natural logs of abundance on time, weighted by the inverse of the variances, yielded an estimate of 3.21% (SE=0.55%) for the annual rate of increase during 1967/68-1987/88 (Fig. 1). The population approximately doubled in size during the 21 yr monitored. The mean annual catch of 174 whales in the Soviet aboriginal fishery (Blokhin 1984, 1989, 1990) represents just under 1% of the mean abundance during this 21 yr period. The combination of increase and catch indicates a mean net productivity of about 4%.

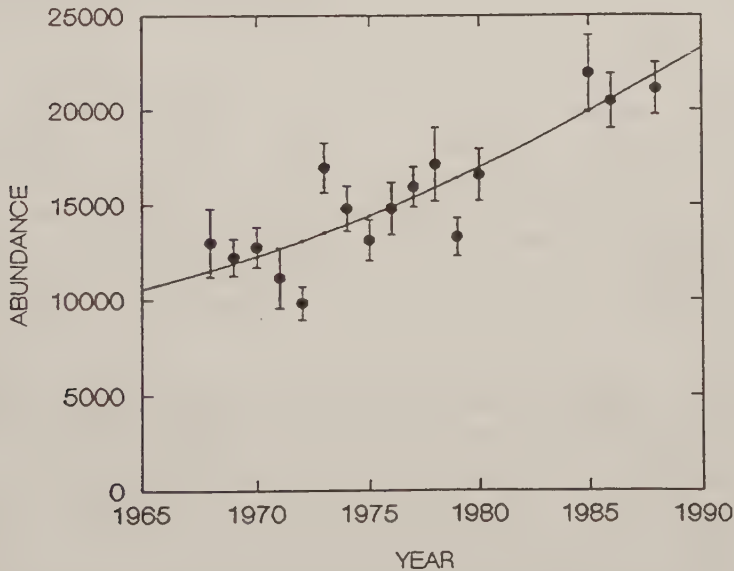


Fig. 1. Gray whale abundance estimates with 95% confidence intervals, by year, from Monterey shore censuses. Fitted line is from exponential regression weighted by reciprocals of squared standard errors (Buckland 1990).

BIOLOGICAL PARAMETERS

Do biological parameters have relevance in determining status of cetaceans? This

question has been debated extensively in recent meetings of the IWC's Scientific Committee (e.g., IWC 1990:119-130). Because of the considerable uncertainty in estimates of biological parameters, it is advisable to use assessment methods that are neither dependent upon nor sensitive to them (de la Mare 1990, IWC 1977). For example, use of the dynamic response method (Goodman 1988) requires only abundance indices. Assessment methods involving the fitting of a population model to abundance data require information on birth and death rates, and on the form of density dependence. A commonly-applied example is "back-calculation" (e.g., Smith and Polacheck 1979), which fits a population dynamics model to a history of catches. The simplest applications of back-calculation collapse effects of birth and death into simple stock-recruitment models. Even for these very simple models it is necessary to examine the sensitivity of results to assumptions about recruitment rates and the form of density dependence.

With some basic, general assumptions about density dependence, the monitoring of trends in one or more biological parameters may provide qualitative (but not conclusive) information on population size relative to carrying capacity (K). It is axiomatic that as a population approaches K , its birth rates will decrease and/or mortality rates will increase. Eberhardt and Siniff (1977) proposed a likely scheme for the direction and order of change in several vital rates as density changes. Unfortunately, we do not yet have adequate data from any cetacean population to test their hypotheses, which were derived from other mammals and theory.

Table 2 lists values of five vital rates accepted by the IWC in its 1990 "comprehensive assessment" of gray whale status (references in Braham and Donovan 1992). Nothing has been published to date allowing the detection of possible changes in mortality rates or ages at sexual maturity. It may be possible to make new estimates of adult mortality rates from the Soviet aboriginal fishery, but this has not been attempted. In contrast, pregnancy rates have been reported for most years' catches since 1965 (Blokhin 1984, 1989, 1990, 1991, Zimushko and Ivashin 1980). Annual reports to the IWC from the past four years (1987-1990) suggested a decline, which would be expected

TABLE 2. Gray whale biological parameters, from the report of the 1990 International Whaling Commission comprehensive assessment of gray whale status (Braham and Donovan 1992).

Gestation period:	418 days
Sexual maturity:	9 yrs median (range 6-12 yrs)
	6 yrs median (range 5-9 yrs)
Ovulation rate:	ca. 00.5/yr
Pregnancy rate:	0.47/yr (0.38-00.56): from catch data, 1965 - 1968
	0.48/yr (0.46-00.50): from photo-ID, 1977 - 1982
Mortality rates:	M = 0.055 (♀ adult): from catch data
	M = 0.046 (♂ adult): " " "
	M = 0.112 (juvenile): from balance equation

to occur in a population nearing K . I combined the available data, estimated simple binomial variances for each annual rate, and plotted the results (Fig. 2a). There does appear to have been a substantial decline in recent years. A linear model exhibits a decline that is significantly different from zero ($F=27.9$, $P<.001$, $r^2=0.76$), but the data are better fit by a non-linear (quadratic) model, as plotted in Fig. 2a ($F=59.3$, $P<.001$, $r^2=0.87$). Fig. 2b shows the pregnancy rates plotted against predicted abundance estimates from Buckland's (1990) exponential model (same as fitted line in Fig. 1). The observed range of rates centered near 0.45 (but with wide confidence limits) during years up to 1986, in agreement with both Rice and Wolman's (1971) estimate of 0.46 from 316 whales captured off California, and Jones (1990) estimate of 0.48 from photo-ID studies.

I fit a simple, generalized exponential model to the pregnancy rate and abundance estimates of Fig. 2b. The specific model used was: $P_t = P_0 (1 - (Nt/K)^Z)$, where P_t is pregnancy rate at time t , $P_0 = 0.5$ is the maximum equilibrium rate (Reilly 1984a), and K is carrying capacity, set speculatively at 25 000 for this exercise (see below). The best fit, drawn in Fig. 2b, was obtained with $Z = 4.4$. If one speculated further that this was the only density dependent vital rate, this would imply that the maximum net productivity level (MNPL, that level which yields maximum net production) $\approx 68\%$ (in the absence of age-structure effects). There are too many untested assumptions in this fitting exercise to use the results for decision making. Nevertheless, it is interesting to note that if K is

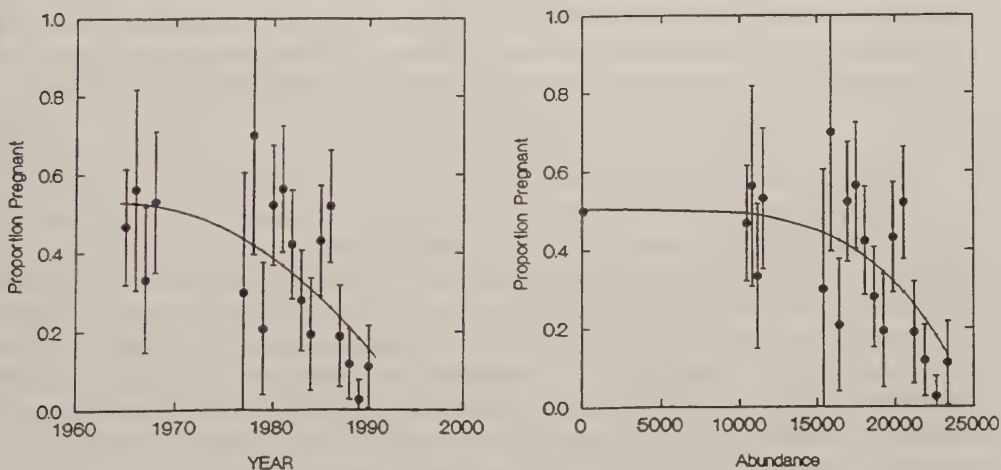


Fig. 2. a. Gray whale pregnancy rates, with binomial 95% confidence limits, by year, from the Soviet aboriginal fishery (Blokhin 1984, 1989, 1990, 1991, and Zimushko and Ivashin 1980). b. Gray whale pregnancy rates with 95% confidence limits by estimated population sizes. Pregnancy rates from Blokhin (1984, 1989, 1990, 1991), Breiwick et al. (1989), and Withrow (1990); abundance estimates from exponential increase model fit to Monterey census data from Breiwick et al. (1989).

in the mid-20 thousands, pregnancy rates appear to be responding similarly to predictions by Fowler (1987) that most density-dependent response is expected to occur in levels above 50% for most large mammals.

A major concern in interpreting the pregnancy rates from the Soviet fishery is possible sampling bias. Blokhin (1989) presents summary tables showing marked differences in pregnancy rates by subarea within the fishery zone around the Chuckchi Peninsula, and a steep decline in rates by month from almost 60% in July to 12% in November. Before the apparent annual trend can be accepted, it is essential that an analysis be conducted to account for effects of location and month of capture. This is not possible given the published summary statistics.

STATUS DETERMINATION

Reference level?

Assessment of a population's status requires agreement upon a reference level, or K , for comparison with the present population level. This is not a problem for populations with a short history of exploitation. For gray whales it is not clear what the reference level should be. Commercial exploitation began in 1846 (Henderson 1972), over 140 yr prior to the most recent census. A further complication arises from the aboriginal fisheries for gray whales, which date back to at least the 16th Century (Mitchell 1979, Mitchell and Reeves 1990). Consequently, the stock was not in an unharvested state in 1846. Ideally, we would be concerned only with the present K , as in the dynamic response method. As discussed below, this method has other limitations for the gray whale case, so we must still select the most appropriate reference level.

Back calculation

This method fits a population dynamics model to a history of catches, back to a point in time prior to exploitation. The abundance at this point is interpreted to be the carrying capacity (Breiwick et al. 1984, de la Mare 1990). Back calculation requires an estimate of current absolute abundance, through which the trajectory must pass, or a series of estimates to be fitted by the trajectory. For gray whales, we have a current absolute abundance estimate, a recent series of abundance estimates, and additional qualitative information to help evaluate trajectories. There is good historical documentation of a rapid decline in abundance following the peak of commercial exploitation, to a state of commercial "extinction" in the late 19th Century (Henderson 1972, 1984).

Early attempts to apply back-calculation to assess the status of gray whales were made by Ohsumi (1976), Reilly (1981), Cooke (1986) and Lankester and Beddington (1986). In general, these efforts were not successful in reconciling the catch history with the current abundance, recent increase, and standard models of density dependence. Reilly (1981) reported one model that appeared to produce a reasonable trajectory, but that result was extremely sensitive to the rather complex modelling structure used.

Butterworth et al. (1990b) repeated this exercise with a simpler population model,

the "hitter-fitter" model of de la Mare (1989), and updated catch statistics. Similar to Reilly (1981) and Lankester and Beddington (1986), this back-calculation explicitly included pre-1846 aboriginal exploitation. Initial runs with just the reported catch levels produced abundance trajectories much like those of the earlier efforts, with a decline during 1967-1981, and a minimum above 12 000 in the late 1800s, clearly not matching available data. Two modifications produced trajectories that were reasonable: a tripling of K during the period (considered very unlikely by the IWC Scientific Committee) or a scaling-up of the catch histories for aboriginal or commercial catches by more than 100%. Even with these changes, a productivity rate (MSY) greater than 3% at MNPL was also required. Estimates of K resulting from the acceptable runs ranged from 23 000 to about 35 000. It seems reasonable to assume that the early aboriginal kills were 100% higher than documented, given the recent, extensive review by Mitchell and Reeves (1990). If accurate, these results indicate the 1988 population of 21 113 was between 70% and about 88% of K . These results alone, however, are probably not sufficient to make a status determination, given the uncertainty involved (Braham and Donovan 1992).

Dynamic response (DR) and related methods

This approach fits simple functions to series of abundance data (relative or absolute) to test for an inflection, under the assumption that such a change in growth rate represents passage through MNPL (Goodman 1988, Gerrodette 1988). The simplest application of the method is to fit a quadratic function and examine the sign of the second order term. Boveng et al. (1988) describe a method of "local" fitting, i.e., to overlapping subsets of the series, followed by examination of the second order coefficients. A growing population passing through MNPL will have positive values initially, then cross the zero line and have negative values. Only positive values indicate status below MNPL.

Gerrodette and DeMaster (1988) applied dynamic response analysis to the 1967-1980 gray whale abundance series of Reilly et al. (1983) and concluded there was evidence that the population passed through MNPL during the sampled period. Boveng (1992) repeated this dynamic response analysis with similar methods, but included the most recent three census points. He concluded that there was no reliable information in the series on the stock's status. Boveng (1992) noted two possibilities to explain this result: the data may be too "noisy" to reflect density-dependent curvature, or the stock may, in fact, have been near MNPL at the midpoint of the sampled interval. Gerrodette (1988) showed that for populations at or somewhat above MNPL the probability of correctly determining status drops to near 0.5.

Butterworth et al. (1990a) applied a variation of the dynamic response method to the same data. They fit logistic and cubic models to the full series (a "global" fit), to test for points of inflection. They found that the cubic model followed what must be local noise in the series, causing spurious, repeated changes in sign of the coefficients. The logistic model fit very similarly to the exponential model shown here in Fig. 1, actually curving upward. Butterworth et al. (1990a) concluded that the probability was not large that the population passed through MNPL during the interval. Based on results of Butterworth et al. (1990a) and Boveng (1992) the dynamic response approach appears to provide little useful information for determining this population's status. It may be, as Boveng notes, that the power of this technique is unacceptably low for populations with

maximum growth rates less than 10% per year.

Goodman (1990) developed and applied a Bayesian approach to determining status from a series of abundance estimates. Unlike the dynamic response analyses, he postulated a modified logistic population dynamics model, and used the data series to improve estimates of K and r (intrinsic rate of increase) from uniform prior distributions set over wide ranges (20 000-50 000 for K , 0.03-0.08 for r). He concluded that there was little additional information in the Monterey census series to improve the prior distributions. The posterior distribution for K had a slight mode at about 23 000, but the distribution was so broad that substantially higher or lower values for K were also quite plausible. Goodman (1990) concluded that, based on the data, it would not be prudent to accept that the true value of K is in any particular subset of the plausible range.

CONCLUSIONS

The dynamic response and related methods have very attractive general properties for status determination: not relying on biological data, and determining status in terms of current K . Unfortunately, they provided little help for the gray whale case. It is difficult to envision another cetacean population for which we will have better abundance indices. In general, these methods may not be appropriate for cetaceans. Perhaps with the addition of more annual estimates there will be sufficient curvature in the abundance series for these methods to succeed.

For the present we are left with both back-calculation results that do not successfully complete a status determination without a substantial modification to the catch record and with MSY rate values that are considered somewhat controversial (e.g., IWC 1977:34). If we accept Henderson's (1972, 1984) careful, conservative reconstruction of the early commercial fishery and its effects on gray whale abundance, likely population sizes in 1846 were in the range of 12 000 to 15 000. The 1988 population was very likely above this range. We must, however, decide if the 1846 population is the appropriate standard, or if we should look even farther back in time prior to aboriginal exploitation. Should preindustrial exploitation by native people be considered part of the natural environment? A more acceptable approach would be to use current K as our standard, but we have no unequivocal, quantitative information about this.

The apparent decline in pregnancy rates is quite interesting and should be verified by a more detailed analysis. There is also some preliminary information cited by Stoker (1990) that the benthic fauna upon which gray whales feed is recently showing signs of over-exploitation. Stoker (1990) stated that recent, unpublished benthic investigations in the Chirikov Basin have noted a significant decline in amphipod populations, particularly of the larger adults, beginning about 1986-1987. If verified, this may be additional evidence that the gray whale population is nearing the limits of its environment.

Recent reviews by the IWC (Braham and Donovan 1992) and International Union for the Conservation of Nature (Klinowska 1991) have concluded that the eastern Pacific population is not in immediate danger of extinction. Gray whales are now legally classified as "endangered" in the U. S. under the Endangered Species Act, but this is

under reconsideration. I see no evidence that this population is in danger of extinction, and agree with the suggestions (e.g., Brownell et al. 1989) to remove it from the "endangered" classification under the U.S. Endangered Species Act. It is not entirely clear where it is in relation to its current K , but the back-calculation assessment and additional, preliminary information suggest that it is probably above MNPL and approaching K .

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**Review of Fishery and Auxiliary Data
for Chilipepper rockfish in the
Eureka/Conception/Monterey INPFC Areas:
a Qualitative Assessment of the Status
of the Stock in 1992**

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Abstract

A qualitative assessment of the stock of chilipepper (Sebastes goodei) indicates that the present Allowable Biological Catch (ABC) of 3,600 mt should be maintained until a quantitative assessment is completed in 1993. Estimated landings have risen in recent years, with 1991 landings exceeding the ABC by about 300 mt. These landings have come primarily from the trawl fishery, but the combined landings from three other fisheries have been substantial since 1984. Length and age frequencies indicated a strong 1984 year class, which entered the trawl fishery in large numbers in 1987, the recreational fishery in 1986, and the hook-and-line and set-net fisheries in 1988. This strong year class will likely influence the fisheries through 1992-1993. Auxiliary data, including biomass indexes from the NOAA triennial cruises and effort data from the recreational fishery, indicated that the stock was stable or increasing at least until 1989. In preparation for the 1993 quantitative assessment, life history parameters for chilipepper were developed.

Introduction

Chilipepper (Sebastes goodei) is a significant component of the California mixed-rockfish fishery. Since 1985, chilipepper trawl landings have exceeded those for bocaccio (Sebastes paucispinis), an important species with which it is often caught (Bence and Rogers 1992). The chilipepper stock is concentrated between Point Conception and Bodega Bay, California (Pearson 1991), so it is not important in fisheries operating north of California.

The most recent assessment for chilipepper was done in 1986 (Henry 1986). That assessment indicated that the stock was moderately exploited and provided no evidence that fishing mortality levels had been increasing over time. The assessment treated landings as coming from a single fishery and used only trawl age-composition data. Since that assessment, the hook-and-line/ long-line and set-net fisheries have increased in relative importance, and there have been substantial revisions in estimates of landings. Furthermore, auxiliary information in the form of an effort time series from the recreational fishery and an index of abundance for NMFS research surveys are now available.

In this document, we present and review the available age-composition, length-composition, landings, auxiliary, and life history data. Our primary objective was to provide a qualitative assessment of the current status of the chilipepper stock in the Conception/Monterey/Eureka INPFC areas. A secondary objective was to lay the groundwork for a quantitative assessment of the stock using the stock-synthesis program (Methot 1989 and 1990), a task we expect to complete during the next year.

Landings

Total estimated landings of chilipepper have varied considerably since 1980 (Figure 1). The landings have been somewhat cyclical since 1982, with estimated landings progressively increasing 1982-1985, decreasing 1985-1987 and increasing again 1987-1991 (Figure 1). The 1991 estimated landings of 3905 mt were higher than the landings in any other year since 1980. A high percentage of the landings came from the trawl fishery in all the years considered, but after 1984 combined landings from the other fisheries were substantial (Figure 1). All the landings were estimated following procedures outlined in Bence and Rogers (1992).

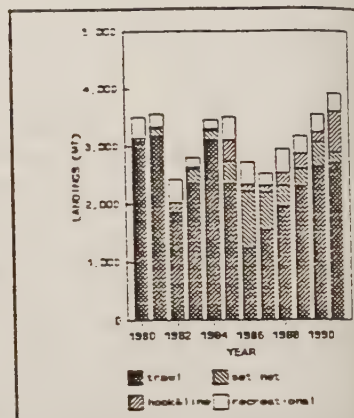


Figure 1. Estimated chilipepper landings.

We estimated that most of the trawl-caught chilipepper were landed in the Monterey area each year (Table 1). By-catch of chilipepper from the offshore Pacific hake (*Merluccius productus*) fishery, as reported by observers on the vessels (Methot and Dorn pers.comm.), are also given in Table 1. The by-catch in 1991 was significant, coming from a relatively few tows in the Monterey area.

Table 1. Estimated trawl landings of chilipepper for the Conception (C), Monterey (M), and Eureka (E) areas; combined with by-catch from the Pacific hake fishery.

YEAR	TRAWL (MT)			BY-CATCH (MT)	TOTAL (MT)
	C	M	E		
1980	327	2698	27		3053
1981	411	2536	241		3189
1982	346	1301	197		1844
1983	275	1853	232		2360
1984	602	2352	155		3109
1985	256	1970	123		2349
1986	172	954	101	2	1229
1987	149	1307	80	1	1537
1988	337	1523	92	2	1954
1989	440	1756	97	4	2297
1990	379	2004	205	48	2636
1991	393	1619	168	522	2702

Estimated chilipepper set-net landings varied from almost none in 1983 to nearly 1000 MT in 1986 (Table 2). There were no set-net landings allowed in the Eureka area, and Monterey landings have exceeded Conception area landings since 1981.

Table 2. Estimated set net landings of chilipepper for the Conception (C), Monterey (M), and Eureka (E) areas.

YEAR	C	M	E	TOTAL
1980	33	6	0	39
1981	100	19	0	119
1982	0	6	0	6
1983	8	227	0	235
1984	12	152	0	165
1985	45	354	0	399
1986	205	775	0	980
1987	252	405	0	657
1988	107	251	0	358
1989	71	228	0	299
1990	114	313	0	426
1991	26	160	0	186

The hook-and-line/long-line fishery landings were usually below 100 MT before 1985 and varied from 157 to 415 MT from 1985 through 1990 (Table 3).

Table 3. Estimated hook caught landings of chilipepper for the Conception (C), Monterey (M), and Eureka (E) areas.

YEAR	C	M	E	TOTAL
1980	43	13	2	58
1981	31	1	0	32
1982	124	49	11	184
1983	30	14	1	45
1984	22	6	0	28
1985	231	104	28	363
1986	34	79	12	125
1987	30	78	13	121
1988	64	133	21	218
1989	91	150	27	268
1990	39	109	22	170
1991	270	381	58	709

Recreational catch of chilipepper has varied from about 150 to 400 mt (Table 4). Recreational landings in 1990 and 1991 were assumed to be the same as the estimated value for 1989. Landings for the recreational fishery for 1980-1989 were obtained in a database from John Witzig (NMFS, Washington D.C.).

Table 4. Estimated recreational catch of chilipepper for Southern and Northern California.

Year	Total
1980	354
1981	220
1982	392
1983	163
1984	157
1985	391
1986	392
1987	206
1988	415
1989	308

Length and Age Frequencies

The length and age frequencies, supplemented by length-at-age data, showed evidence of a strong 1984 year class. All length and age frequencies (Figures 2-7) are presented at the end of this document. The 1987 trawl fishery length frequencies indicated a high percentage of small fish (Figure 2). This group was associated with a distinctive mode in total length (tl), particularly for the females (30-32 cm). This mode could be traced moving to progressively larger sizes in 1988-1991 (Figure 2). The age frequencies indicated that this was the 1984 year class, since there was a high percentage of three year old fish in 1987 and four year old fish in 1988 (Figure 3). The trawl length-at-age data for 1987 confirmed the relation, with a mean tl of 32.6 cm for three year old females. If the 1984 year class follows the pattern of the strong 1975 year class evident in the age frequencies (Figure 3), it would be expected to have a large influence on the trawl fishery only until age 8 or 9 (1992 or 1993).

The 1984 year class evidently entered the other fisheries/cruise at ages 2 or 4 rather than age 3. Evidence of the strong year class was less distinct in the other data sources, but in 1988 there appeared to be a substantial group entering the set-net (female mode 36 cm tl) (Figure 4) and hook-and-line fisheries (female mode 38 cm tl) (Figure 5). The trawl length-at-age data for 1988 had a mean size of 36 cm for four-year-old females. The recreational data was not separated by sex, so year classes were blurred (Figure 6). There was, however, some sign of a shift to

younger fish which began in 1986 and a strong mode at progressively larger sizes in the following years. The 1986 triennial cruise data showed the capture of a large group of young fish, with a mode of 26-28 cm tl for females (Figure 7). This is likely the 1984 year class, although they are larger than expected for two-year-old fish based on length-at-age data from the 1977-triennial cruise.

As evidenced by the various years in which the 1984 year class was evident in the different sources of data, the selectivities varied to an extent depending upon the type of fishery/cruise. The recreational fishery and the triennial cruises caught a higher percentage of small fish (20-30 cm tl) than did the trawl, hook and line, and set net fisheries (Figures 6 and 7 versus Figures 2, 4 and 5), a pattern that was also evident in our analysis of bocaccio data (Bence and Rogers 1992). The set-net fishery caught a higher percentage of larger fish (> 40 cm tl) than did the trawl for a given year (Figure 2 versus Figure 4). This was also true for the hook-and-line fishery in the years prior to 1990 (Figure 2 versus Figure 5). Hook-and-line length frequencies were based on a smaller number of fish than those for the other fisheries, and so were less smooth. In all cases where data were separated by sex, the female lengths tended to have a wider range than did the males, and the average female caught was generally larger than the average male.

Auxiliary Data

The triennial survey abundance indexes and the recreational CPUE estimates indicated that the chilipepper stock remained stable 1980-1987 and may have increased 1988-1989 (Table 5), perhaps due the large 1984 year class. The estimated abundance based on the 1989 triennial cruise was considerably higher than the previous surveys. The CPUE for the recreational fishery also increased substantially in 1988 and 1989.

Table 5. Available auxiliary data regarding the chilipepper stock for the period 1980-1991.

YEAR	RECREATIONAL (CPUE)	TRIENNIAL INDEX (SE)
1980	0.35	10362 (5137)
1981	0.68	
1982	0.34	
1983	0.28	9399 (4399)
1984	0.27	
1985	0.56	
1986	0.45	10911 (2544)
1987	0.45	
1988	1.00	
1989	1.41	16615 (4969)

Life History Parameters

Our primary goal in developing the life history parameters was to lay the groundwork for a quantitative assessment of chilipepper using the stock-synthesis model or a related approach. In practice, the synthesis model, like all catch-at-age methods, requires an a-priori estimate of natural mortality. Since we will be using the size-based version of the synthesis model, we also need relations between mean length and age, coefficient of variation in length-at-age and age, and length and weight. The first two relations allow the synthesis model, given an estimate of the population numbers at age, to generate estimates of the population numbers at length. The third relation allows the model to translate catches in terms of numbers at length into biomass, which can be compared to observed landings. Additional relations between the proportion of the female population that is mature and length, and mass-specific fecundity and weight, although not required for the modeling, are useful in judging the current status of the stock. They allow the model's estimate of the stock-composition in terms of size and age to be translated into total spawning potential, where the spawning capacity of the stock is defined as the total number of eggs carried by the female population.

Although natural mortality can not be precisely estimated, a range of 0.15 to 0.20 seems reasonable. A natural mortality of 0.20 was suggested for chilipepper by Henry (1986) on the basis of a maximum age of 29 years, a von Bertalanffy k factor of 0.18, the proportion of very old fish in the population, and values for other rockfish. The other end of our range is closer to 0.13, which was the total mortality rate (Z) predicted using Hoenig's (1983) relation between Z and the maximum age (35 years) found when considering a substantial number of trawl samples.

The synthesis model has the ability to estimate a growth model internally, making use of length-at-age data. We explored the relation between length and age using a broader range of data than we could use in the model, as a method of obtaining starting values and reasonable ranges for the parameters. Growth curves for each sex were derived by fitting a form of the von Bertalanffy equation proposed by Schnute and Fournier (1980) using non-linear regression. This equation was:

$$Length_{age} = L_A + (L_M - L_A) \frac{(1 - e^{(-k(age-A))})}{(1 - e^{(-k(M-A))})}$$

where the estimated parameters are k , and L_A and L_M , representing expected mean total lengths at two ages ($A < M$). We used age 1 for

A and age 14 for M. Age 14 was chosen for M rather than the maximum age in the samples because it produced lower mean square errors and correlations between parameters. Cerrato (1991) found that nonlinearity of the model; which generally results in biased, nonnormal parameter estimates; is greatly reduced when using an intermediate rather than maximum age for M. The resulting equations provided a good fit to the data (Figure 8).

After fitting the equation, lengths at infinite ages were calculated:

$$L_{\infty} = L_A - (L_A - L_M) e^{(k(1-M))}$$

The resulting values which could serve as initial values for the parameters in the synthesis model were:

♀ $L_{\infty}=52$ cm, $k=-0.20$, $L_1=17.4$ cm
 ♂ $L_{\infty}=39$ cm, $k=-0.28$, $L_1=18.4$ cm.

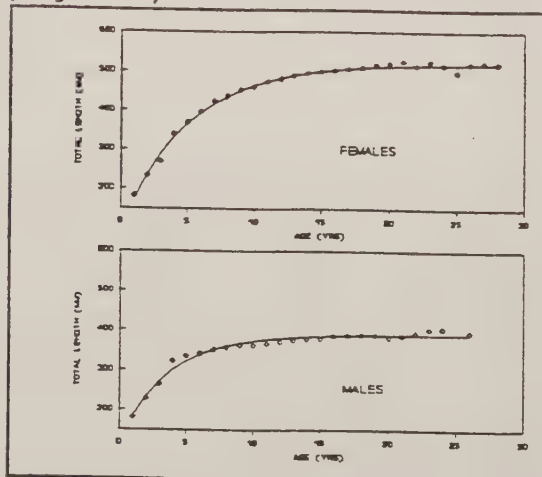


Figure 8. Fit of the growth curve

Each mean used to fit the von Bertalanffy equations was derived from samples of greater than ten fish, which came from a triennial cruise for ages 1-5 and from the trawl fishery for ages greater than five. These were selected from the available data (Figure 9) as being most representative of the population. The trawl data were from 1980-1988, the triennial data from 1977, and the sport fishery data from fish caught on party boats 1980-1984. The triennial cruise data were used for the younger ages because they provided the only available information for age 1 and the fish were collected using a smaller mesh size, decreasing the probability of selecting only the larger fish for a given

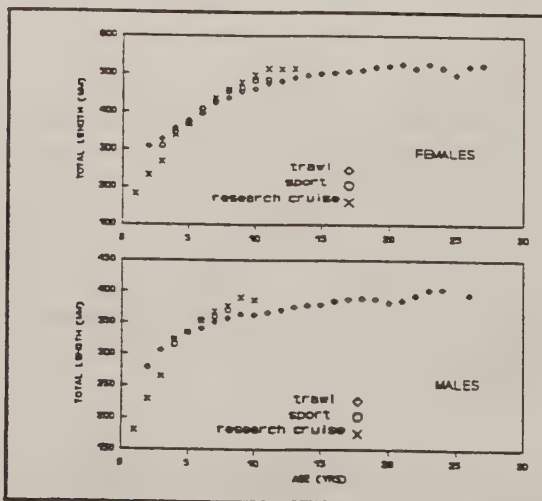


Figure 9. Available Length at Age Data.

age. The trawl fishery data were used for the larger ages because they were based on samples from a wider range of years, including more recent data, and were all that were available for ages greater than 15. The sport data were not used because they spanned only a few ages and the selectivity was unknown. The reason for the larger size at age in the sport and triennial data versus the trawl data for ages of about 7-15 years may be due to year effects or to different ageing methods (break-and-burn for the trawl 1982-1988 versus surface for the other years and data sources). The trawl data indicated that fish about 7-15 years in 1980 and 1981 were a larger size at age than in the subsequent years.

The linear regressions describing the relations between coefficient of variations in length at age (CV) and increasing age for each sex were fit to CV from samples of greater than 10 fish at age from the trawl fishery, using ages 3-21 (Figure 10). These data were selected because cv's from other ages or from the triennial cruise in 1977 were widely scattered, and we were primarily concerned with the ages in the range chosen. The resulting regressions, significant at $p < 0.05$, were:

$$CV_{age}^f = 9.090 - 0.238 * age$$

$$CV_{age}^m = 8.285 - 0.207 * age$$

Estimates of CV for the minimum and maximum ages used in the model will be derived using those equations.

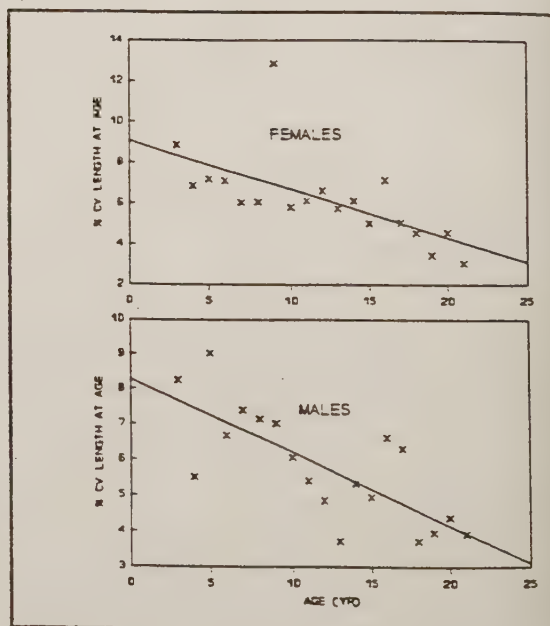


Figure 10. Fit to CV Trawl Data

Phillips (1964) gave parameters for a length-weight exponential equation, which we converted to predict weight in kg from total length in cm.

Parameters from an equation relating the proportion of females mature as a function of age were taken from Echeveria (1987), who estimated 50% maturity at 34 cm.

The relation between the mass specific fecundity and weight of the female fish (kg) was described by fitting a linear regression to derived data (Figure 11). The data were derived using information presented by Phillips (1964) on the number of eggs in female chilipepper of different lengths. We converted the lengths to weights using the regression supplied in the same paper. The regression fit to the derived data ($p < 0.05$) was:

$$\frac{\text{million eggs}}{\text{kg}} = 0.0926 + 0.0428 * k$$

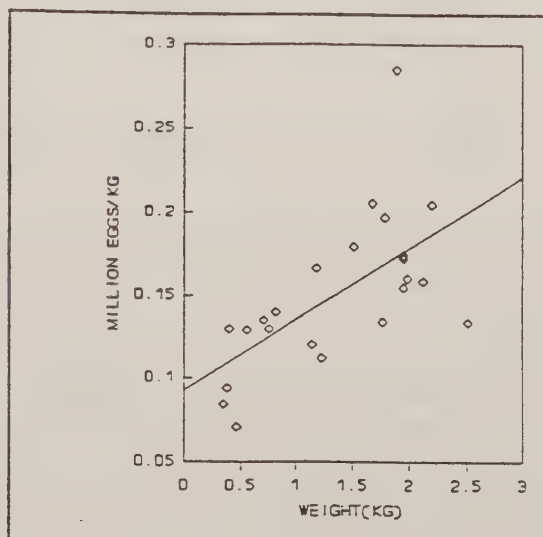


Figure 11. Fit to data from Phillips (1964).

Conclusions

The chilipepper stock, at least through 1989, appeared to be stable or increasing. The increase in landings since 1987 could be supported by the presence of a strong 1984 year class. The last strong year class (1975) apparently remained dominant in the trawl fishery until it was 8-9 years old. If this holds true for the 1984 year class, it would be expected to influence the trawl fishery in 1992-1993, but to a lesser extent than in recent years. The present ABC of 3,600 mt is less than the estimated 1991 landings of 3,905 mt. Without evidence of more recent strong year class entering the fishery, raising the ABC would not be justified in 1992. We recommend the keeping the ABC at the present level until a quantitative assessment is done in 1993.

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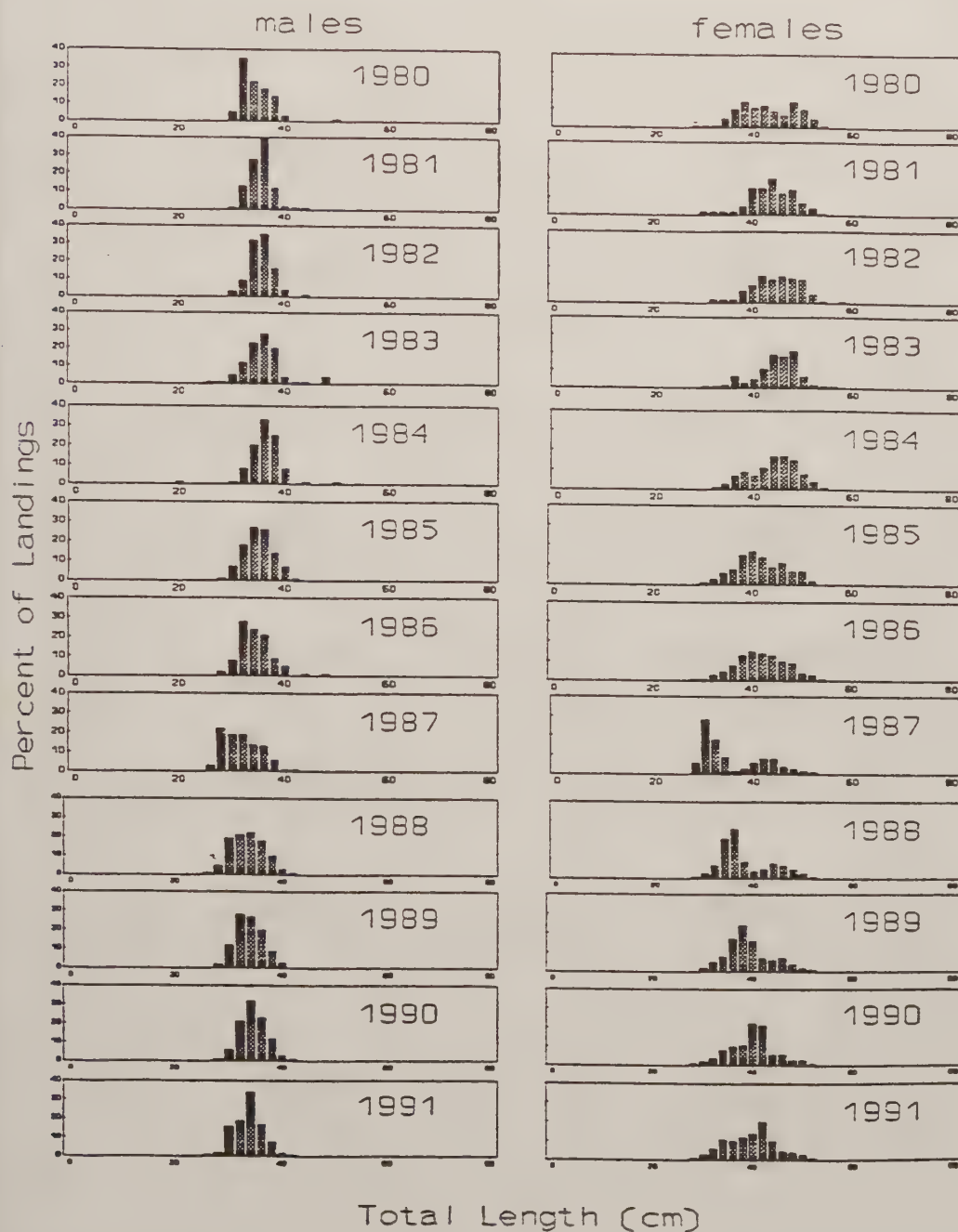


Figure 2. Length composition data for chilipepper based on samples from the California trawl fishery landings.

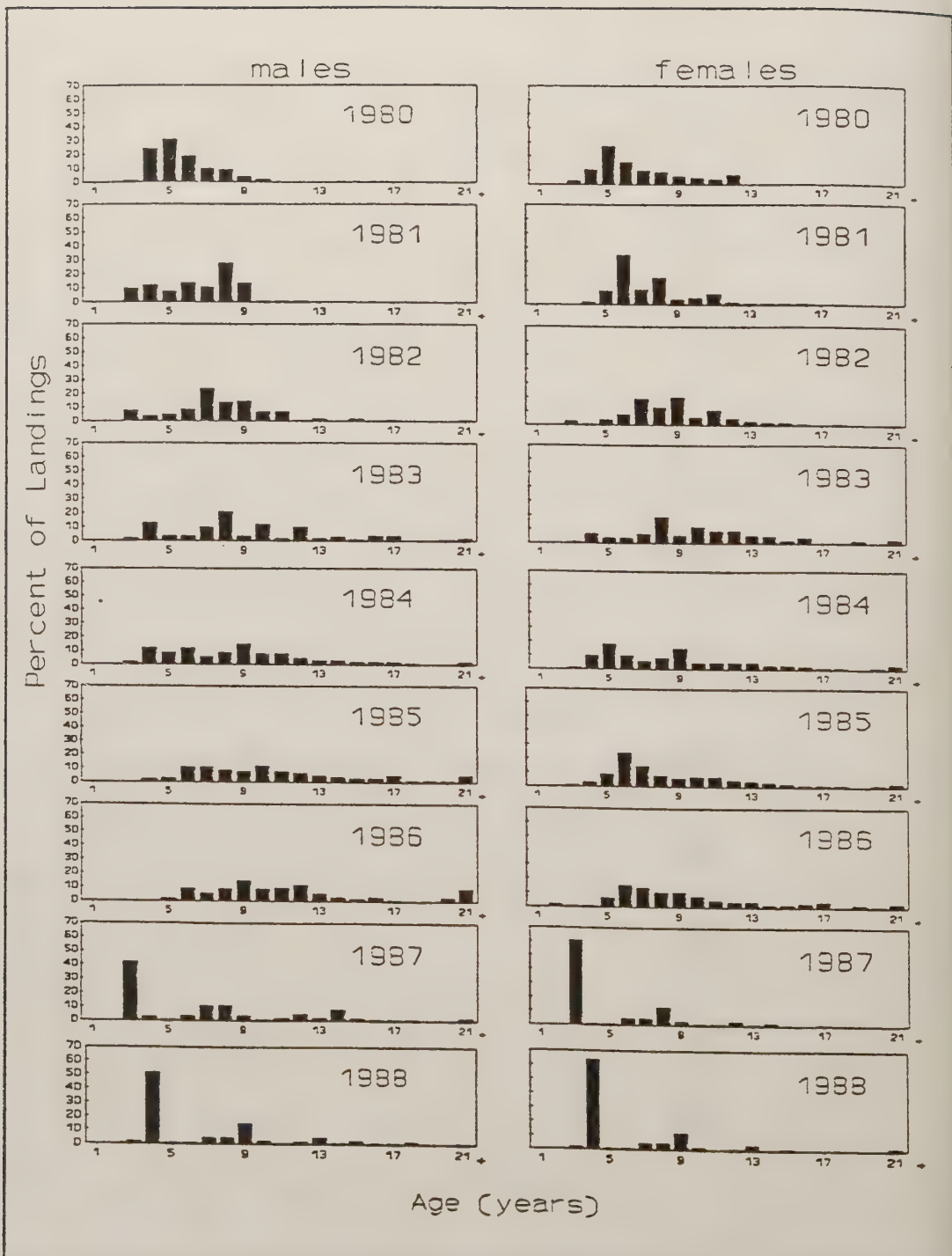


Figure 3. Age composition data for chilipepper based on samples from the California trawl fishery landings.

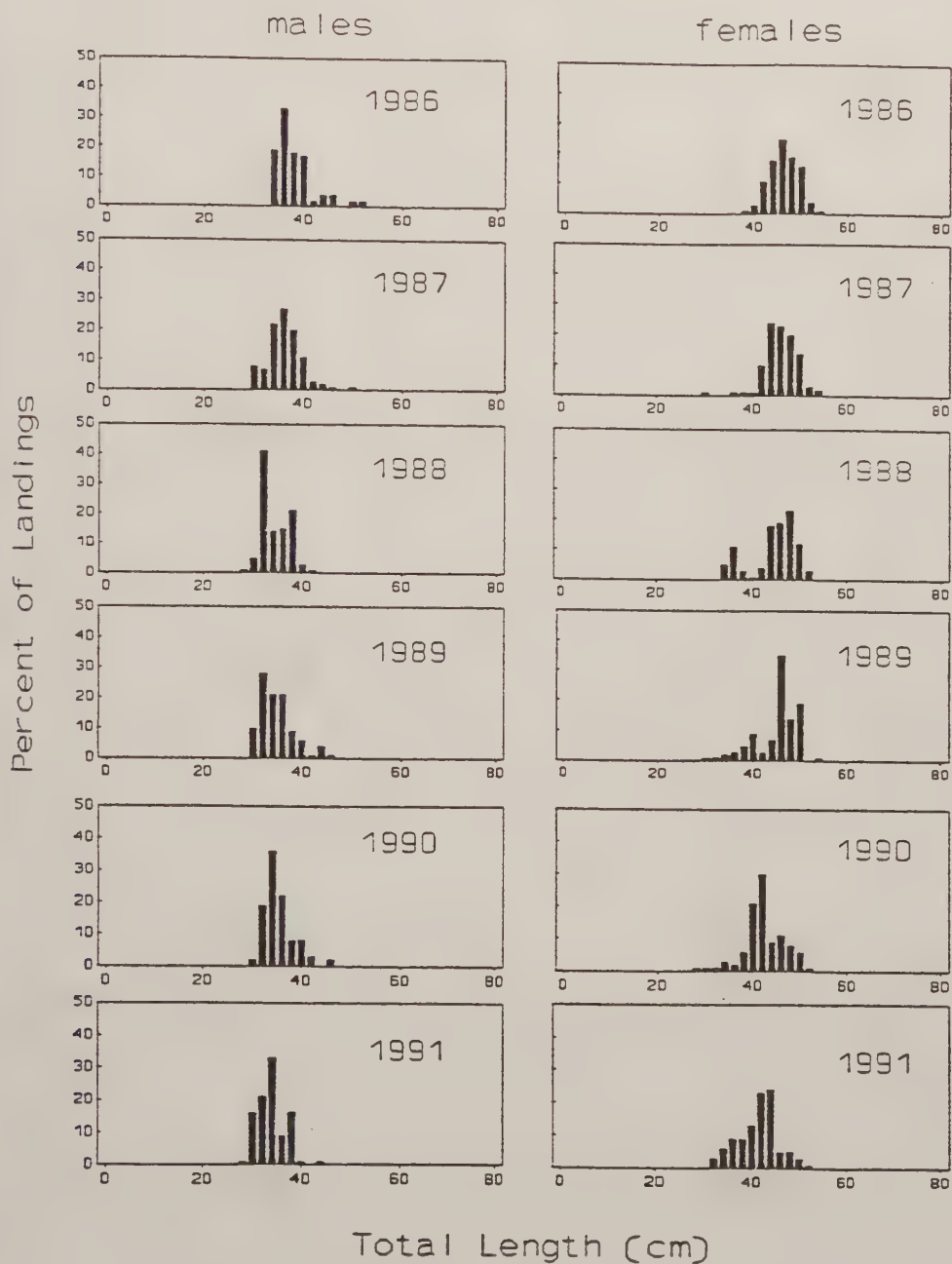


Figure 4. Length composition data for chilipepper based on samples from the California set-net fishery landings.

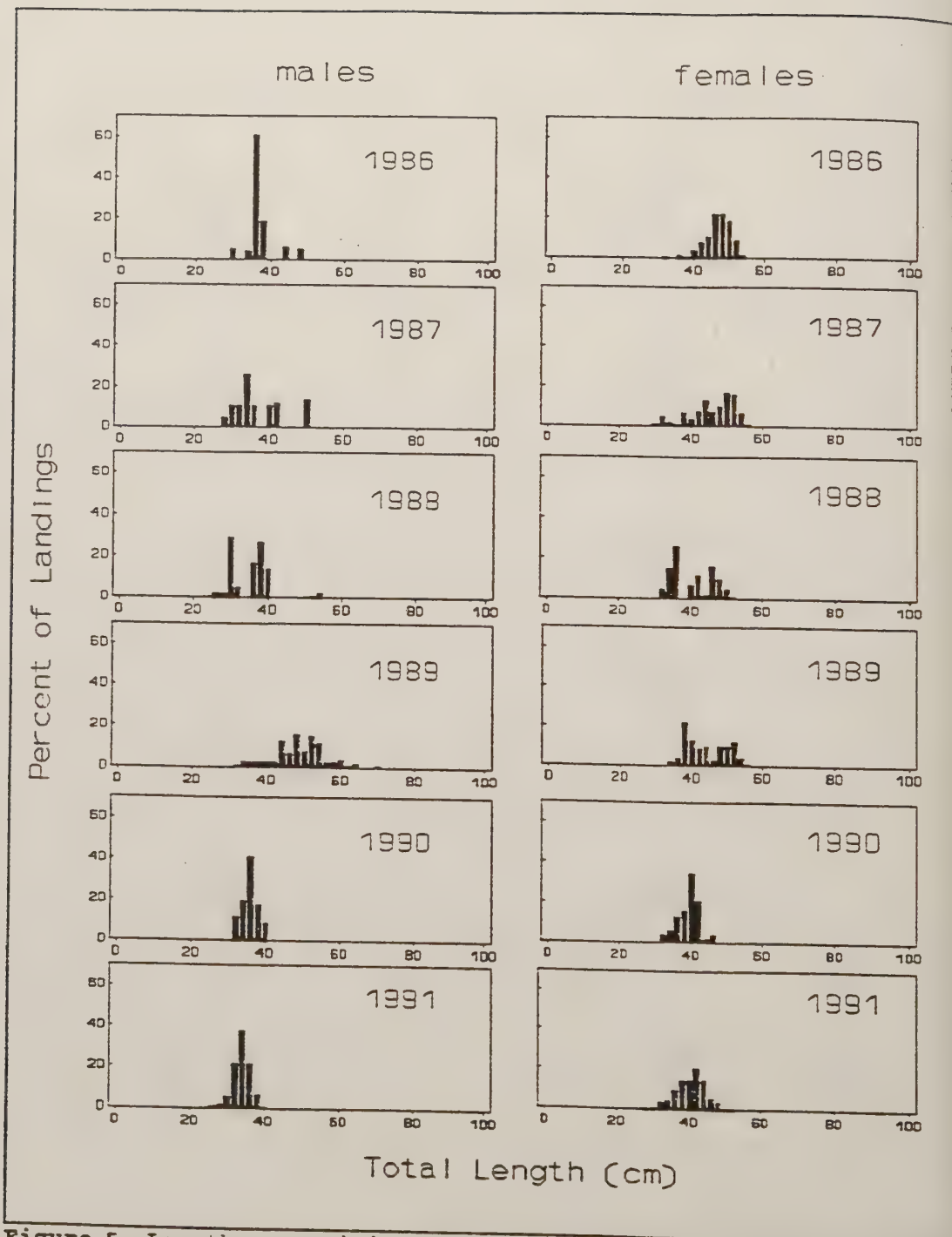


Figure 5. Length composition data for chilipepper based on samples from the California hook and line fishery.

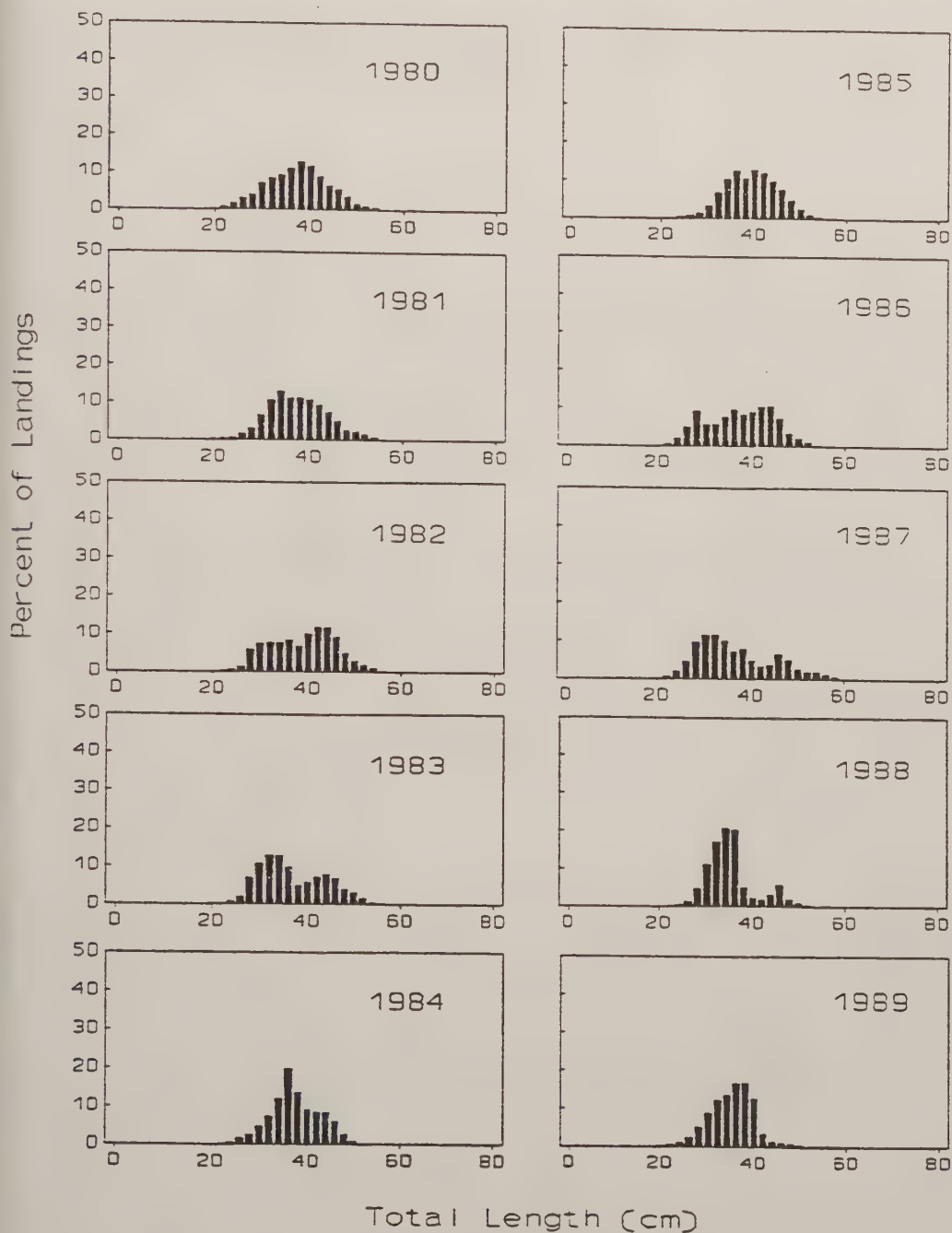


Figure 6. Length composition data for chilipepper based on samples from the California recreational fishery landings.

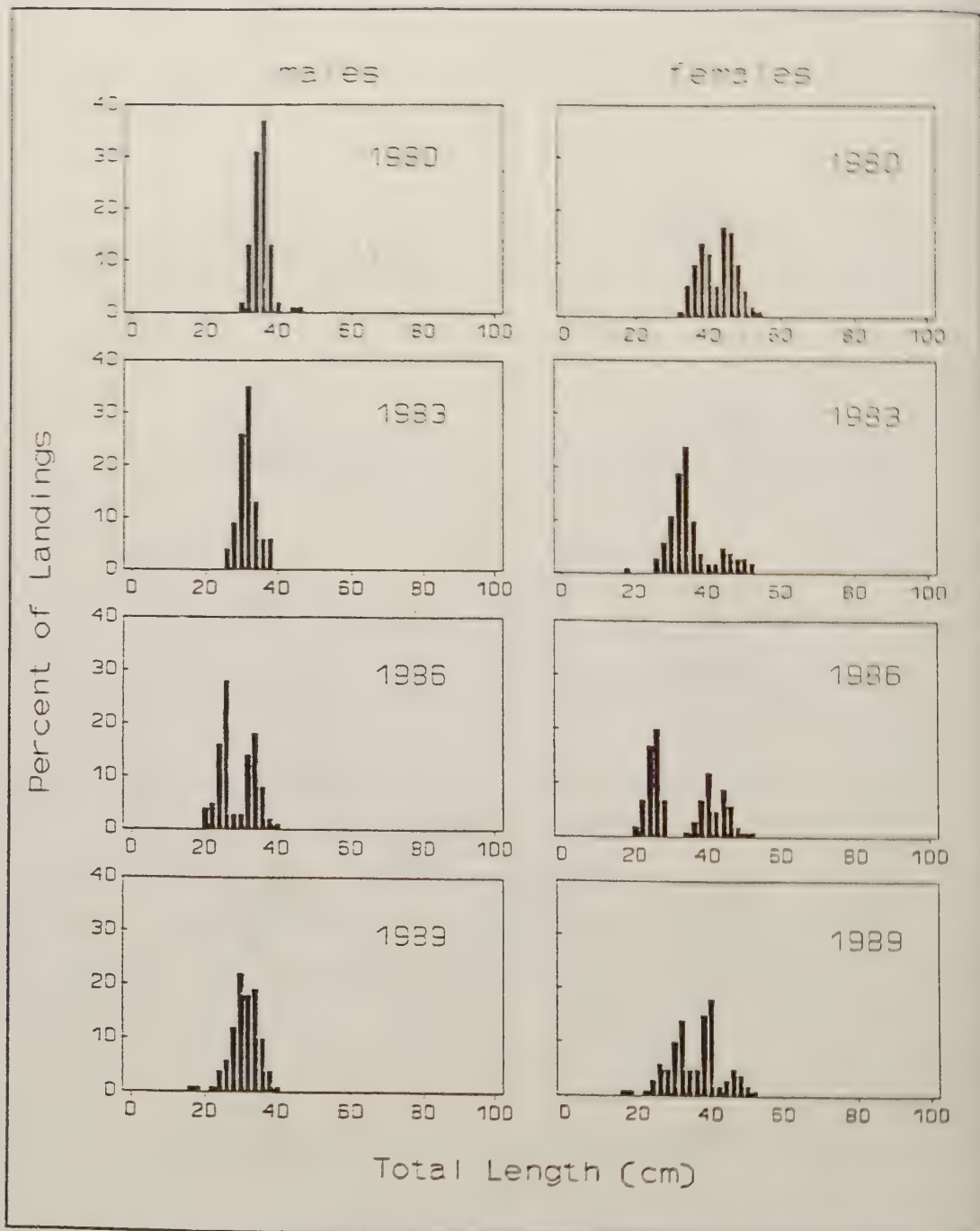


Figure 7. Length composition data for chilipepper based on samples from the NMFS triennial bottom trawl surveys.

Numerical Definition of Groundfish Assemblages Caught Off the Coasts of Oregon and Washington Using Commercial Fishing Strategies

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Rogers, J. B., and E. K. Pikitch. 1992. Numerical definition of groundfish assemblages caught off the coasts of Oregon and Washington using commercial fishing strategies. *Can. J. Fish. Aquat. Sci.* 49: 2648–2656.

Numerical definition of species caught together by the groundfish trawl fishery operating off the Oregon and Washington coasts during 1985–87 indicated six major assemblages of species. Observers on commercial vessels recorded data allowing estimation of the weights of commercially important species caught in each tow. Assemblages were selected based on consistencies in three types of analysis of the species weights: detrended correspondence ordination, two-way indicator species clustering, and Bray–Curtis group average clustering. Two of the assemblages were dominated by a single species, one consisting largely of smooth pink shrimp (*Pandalus jordani*) and the other primarily of widow rockfish (*Sebastes entomelas*). The other assemblages identified were a deepwater rockfish assemblage, a deepwater Dover sole assemblage, a nearshore mixed-species assemblage, and a bottom rockfish assemblage. These assemblages of commercially cooccurring species may be treated as units in developing mixed-species management plans. The deepwater rockfish assemblage we identify has not been previously described.

La définition numérique des espèces capturées par les chalutiers qui pêchaient le poisson de fond au large des côtes des États de l'Oregon et de Washington au cours de la période 1985–1987 a indiqué six assemblages d'espèces principaux. Des observateurs se trouvant sur des navires commerciaux ont relevé des données permettant l'estimation des poids des espèces commercialement importantes capturées dans chaque trait. Les assemblages ont été choisis en fonction de la conformité dans trois types d'analyse des poids des espèces : ordination de correspondance à tendance temporelle éliminée, groupement des espèces à indicateur double et groupement de moyenne de groupe de Bray–Curtis. Deux des assemblages étaient dominés par une seule espèce, un consistant largement en crevettes océaniques (*Pandalus jordani*) et l'autre principalement en veuves (*Sebastes entomelas*). Les autres assemblages identifiés étaient : un assemblage de sébaste d'eau profonde, un assemblage de sole de Douvres d'eau profonde, un assemblage d'espèces mélangées situé près du rivage et un assemblage de sébaste de fond. Ces assemblages d'espèces présentes commercialement présentes simultanément peuvent être traités comme des unités dans l'élaboration de plans de gestion d'espèces mélangées. L'assemblage de sébaste d'eau profonde que nous avons identifié n'avait pas été décrit précédemment.

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The trawl fishermen operating off the coasts of Oregon and Washington often catch mixed species of groundfish including rockfishes and thornyheads (Scorpaenidae), Pacific whiting (Pacific hake) (*Merluccius productus*), flatfishes (Pleuronectidae and Bothidae), and sablefish (*Anoplopoma fimbria*). Although in the past, these fishes have been managed on an individual species basis, it is now recognized that this can result in excessive waste of incidental catch or overharvest of the least productive species (Paulik et al. 1967; Pikitch 1991). Managers have begun to set trip limits based on species complexes (PFMC 1990), and mixed-species models have been developed to assess the effects of technological interactions (Murawski 1984; Pikitch 1987a). To be effective, these approaches require accurate knowledge of which species are consistently caught together.

Based on qualitative knowledge of the fishery, we would expect five major assemblages of species in the commercial catches. Using information from managers and fishermen, Pikitch et al. (1988) described five major West Coast groundfish strategies which target (intend to catch) different assemblages. Assuming that strategies are accurate and effective, the assemblages caught by the trawl fishery would include (1) a bottom rockfish assemblage (BRF) consisting of rockfish (*Sebastes* spp.), (2) a midwater assemblage (MID), including widow rockfish (*Sebastes entomelas*) and Pacific whiting, (3) a deepwater Dover sole assemblage (DWD), primarily Dover sole (*Microstomus pacificus*), along with sablefish and thornyheads (*Sebastolobus* spp.), (4) a nearshore mixed-species assemblage (NSM) consisting of flatfish, and (5) a shrimp assemblage (SHR), primarily smooth pink shrimp (*Pandalus jordani*).

Quantitative definition of trawl assemblages for the area has been accomplished using research or logbook data, but the resulting assemblages may not accurately represent those caught commercially. Research data analyzed by Alverson (1953),

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Hitz and Alverson (1963), Day and Pearcy (1968), Pearcy (1978), Gabriel and Tyler (1980), Pearcy et al. (1982), and K. L. Weinberg (AFSC NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070, unpubl. data) were generally collected using standardized strategies with one or two gears. The commercial fishery uses six gears and probably operates with a variety of strategies (Pikitch et al. 1988). Logbook data, analyzed by Tyler et al. (1984) and Rickey and Lai (1990), do not include discarded fish, have low resolution for rockfish species, and have not been verified for accuracy or consistency. Prior definitions using both types of data are difficult to assess for accuracy, since they generally relied on one or two methods of analysis, which varied between studies.

Quantitative definition using unbiased data and consistencies among a variety of methods of analysis could provide managers and modelers with a more accurate description of the commercially caught assemblages and help assess the previously defined commercial strategies. Data collected by observers on commercial vessels would be relatively accurate and unbiased, assuming that fishermen's behavior on boats that allow observers is representative of commercial fishing behavior. Assemblages determined using a combination of ordination and classification techniques would have greater reliability than definition based on any one method alone (Gauch 1980; Gabriel and Murawski 1985). Consistencies between methods could also allow determination of a few assemblages which reflect major sources of variation in the data, without relying on knowledge of external factors, such as correlation with environmental variables.

The specific objectives of this research were to (1) quantitatively define assemblages of fish caught in the commercial trawl fishery off the coasts of Oregon and Washington using data collected by observers on commercial vessels, (2) assess the accuracy/effectiveness of the strategies described by Pikitch et al. (1988) by comparing tows designated by strategy with tows designated by the defined assemblages and, (3) develop a method of using consistencies in three data analysis techniques to select the assemblages.

Materials and Methods

Data Collection

Observers of normal fishing operations on commercial fishing vessels collected the data (1469 tows) during 1985–87 (Pikitch 1987b). The northern and southern boundaries of the study were 48°42' and 42°60' latitude, respectively, primarily within the INPFC Columbia Management Area. Participation in the study was voluntary and included vessels using bottom, midwater, and shrimp trawls. The skipper and/or observer visually estimated the total weight of the catch from a single tow. The observer then took a random sample from each catch, or examined the entire catch if the total weight was sufficiently small. The weight of each species retained or discarded in the sample was recorded. Total weights of the various species kept or discarded in the catch were estimated by multiplying the sampled weight of the species by the ratio of the total catch weight to the total sample weight. Based on the gear used, depth fished, and species targeted, observers designated a predefined trawling strategy (Pikitch et al. 1988) for each tow. To clarify the distinction between the strategies and the assemblages they are expected to catch, which were described earlier, we added an S in front of the acronyms used by Pikitch et al. (1988) when referring to the strategies. These strategies were (1) bottom rockfish trawling (SBRF): tows conducted

using roller gear on the ocean bottom, with rockfish as the intended catch, (2) midwater trawling (SMID): tows conducted using midwater trawl gear above the bottom, targeting on widow rockfish and Pacific whiting, (3) deepwater Dover trawling (SDWD): bottom tows conducted in areas exceeding 183 m, using mud gear, roller gear, or mud–roller combination gear, with targeting primarily on Dover sole, along with sablefish and thornyheads, (4) nearshore mixed-species trawling (SNSM): tows conducted using mud gear on the bottom in less than 183 m with flatfish as primary targets, and (5) shrimp trawling (SSHR): tows conducted using shrimp gear, targeting on pink shrimp.

Data Preparation

We used a data base consisting of total species weights in each catch and corrected and reduced the data base by eliminating certain tows and species. Ranges, plots, and charts of the data were examined and outliers that were obvious errors were removed. To fit the available clustering capacity (amount of computer memory) and make the results more interpretable, we used only those species deemed commercially important in defining assemblages. The species selected were those that the fishermen identified as target species or those species that composed at least 1% of the estimated total of all catches sampled. We eliminated tows without any catch, lacking a sample, or missing information on the weight of a species. Tows with missing weights of Pacific halibut (*Hippoglossus stenolepis*) or Pacific salmon (*Oncorhynchus* spp.) were not eliminated. Observers usually did not weigh those two species, as it was illegal to retain them onboard.

Description of Analyses

We analyzed the data using an ordination technique and two opposite types of hierarchical classification techniques. Ordination was used to represent catch and species relationships in a low-dimensional space (Gauch 1980). Hierarchical classification was used to place catches into groups, with relationships among groups demonstrated by a dendrogram (Gauch 1980). We employed two types of hierarchical classification: agglomerative, which starts with individual hauls and progressively combines them, and divisive, which starts with all the hauls and progressively divides them.

For ordination, we selected detrended correspondence analysis (DCA) (Hill 1979a), which is a modification of reciprocal averaging and iteratively maximizes the correspondence between the species and catch ordinations. DCA derives a series of ordination axes. Each axis consists of a set of species scores and a corresponding set of catch scores, which are weighted averages of the species scores (Hill and Gauch 1980). Each axis has an eigenvalue which represents the amount of correspondence between species and catch scores on that axis. The axes are scaled so that on a species axis, a species may be expected to appear, rise to its mode of abundance, and disappear in about 4 units, and on a catch axis, a full turnover in species composition occurs over 4 units (Hill and Gauch 1980). DCA is preferable to other ordination techniques in that it does not require a linear relationship between species and catches, eliminates any systematic relationship between the series of ordination axes, and scales the axes so that the dispersion of species scores within samples is constant.

The hierarchical agglomerative technique used to classify the hauls was based on the Bray–Curtis dissimilarity index (Bray and Curtis 1957) with group average fusion criteria (Sneath and

Sokal 1973).³ The Bray–Curtis index has been used extensively in marine ecology (Boesch 1977) and tends to be good at reflecting abiotic aspects (Clifford and Stephenson 1975). Group average fusion is the most widely used clustering method in aquatic ecology and introduces relatively little distortion to the relationships expressed in the matrix (Boesch 1977).

The hierarchical divisive clustering technique used was two-way indicator species analysis (TWINSPAN) (Hill 1979b). TWINSPAN was selected because it uses information on all the species (it is polythetic rather than monothetic), provides an objective method of splitting ordinations, and has minimal computer space and time requirements (Gauch 1980). TWINSPAN operates by dividing ordinations in half. It constructs three ordinations: a "primary" ordination using reciprocal averaging, a "refined" ordination using as a basis the species preferential to one side or the other of the primary ordination, and an "indicator" ordination based on only the most highly preferential species. The refined ordination generally determines the division, while the indicator ordination describes it. To account for differences in abundance, we designated cutoff values so that each species could be treated as four separate "species", based on abundance in the haul. Since cutoff values had to be the same for all species, we computed the means of target species abundances and designated cutoff values as absence of catch, the minimum of the target species means, the mean of target species means, and the maximum mean.

Assemblage Determination

To look for consistent assemblage patterns in the three methods of data analysis, we first determined the maximum number of clusters to consider for each clustering method. We utilized dendrograms, illustrating the way groups hierarchically combined or divided, with the number of clusters increasing with decreasing levels on the dendrograms. We began by selecting a level of agglomeration or division which resulted in two groups of catches and used those cluster designations on plots of the DCA catch scores. We plotted the DCA catch scores for two axes at a time (x and y), with each catch designated by cluster. This was done for both the Bray–Curtis and TWINSPAN cluster designations. The levels were then changed to increase the number of groups until the cluster designated for catches with scores near one end of each DCA axis was different than the cluster designated for the catches with scores near the other end of the axis. If the groups did not separate similarly to the axis scores at any level of clustering, the axis was not used. At each level of clustering, we only considered catch groups that contained more than 1% of the catches. Clusters with less than 1% of the catches were not split off in the TWINSPAN clustering and were eliminated from the Bray–Curtis clustering.

After the maximum number of clusters to consider was determined, clusters were combined or recombined to higher levels on the dendrograms to achieve consistency in catch placement on the DCA axes between the two methods of clustering. This was done given that different clusters were still associated with opposite extremes of the selected DCA axes. For instance, at the minimum levels on the dendrograms, the Bray–Curtis clustering might have determined one cluster for a given area on a DCA axes plot and TWINSPAN two clusters in the same area. If those two clusters recombined to one cluster at a higher level

on the TWINSPAN dendrogram, that level was selected. If consistency could not be achieved while maintaining different cluster designations for catches with scores near opposite ends of the axes, a cluster was considered an inconsistent assemblage.

We then compared the species associated with the selected DCA axes and the selected catch clusters for each clustering method. The species associations with the catch clusters were emphasized rather than species clusters themselves, since we desired species to be allowed to associate with more than one group. Plots of DCA species scores on the selected DCA axes were examined and species associated with the clusters were outlined on the plots. For the Bray–Curtis catch clusters, we examined two measures of species association. One measure expressed which species were caught in the greatest abundance (percentage of total weight in the cluster). The second measure indicated additional species which, although in low abundance in all clusters, were caught selectively in certain clusters (average weight in a cluster divided by the average weight caught in all the clusters) (Boesch 1977). For TWINSPAN, we looked at the indicator species for each cluster.

The defined assemblages were then assigned names based on their similarity to assemblages expected from the strategy definitions. A table was derived showing the number of tows for each combination of strategy and assemblage designation. An assemblage was given the name and acronym of the expected assemblage if most of the tows placed in that assemblage were designated as that strategy and the species associated with the assemblage were similar to the species expected given that strategy. If there was not a strong agreement between an assemblage and any one strategy, the assemblage was given a name based on the species associated with it.

Results

Preliminary Analysis

The species abundance data matrix on which we based the analyses contained information on 1351 of the 1469 tows and 26 of the 178 species found in the catches. Five species were not identified as target species, but had total catches greater than 15 323 kg, which was 1% of all the weight sampled. Those species were longnose skate (*Raja rhina*), spiny dogfish (*Squalus acanthias*), Pacific whiting, sharpchin rockfish (*Sebastes zacentrus*), and yellowmouth rockfish (*Sebastes reedi*). Six species were identified as targets by the fishermen, but did not constitute at least 1% of the total catches sampled: sanddab (*Citharichthys* spp.), starry flounder (*Platichthys stellatus*), sand sole (*Psettichthys melanostictus*), Pacific cod (*Gadus macrocephalus*), bocaccio (*Sebastes paucispinis*), and yelloweye rockfish (*Sebastes ruberrimus*). The remaining 15 species were targeted and constituted >1% of the catch. These comprised arrowtooth flounder (*Atheresthes stomias*), petrale sole (*Eopsetta jordani*), English sole (*Pleuronectes vetulus*, previously *Parophrys vetulus*), Dover sole, rex sole (*Errex zachirus*, previously *Glyptocephalus zachirus*), sablefish, lingcod (*Ophiodon elongatus*), shortspine thornyhead (*Sebastolobus alascanus*), Pacific ocean perch (*Sebastes alutus*), darkblotched rockfish (*Sebastes crameri*), splitnose rockfish (*Sebastes diploproa*), widow rockfish, yellowtail rockfish (*Sebastes flavidus*), canary rockfish (*Sebastes pinniger*), and smooth pink shrimp.

We eliminated a total of 118 tows from the species abundance matrix: three tows had uncorrectable errors, there was no sample in 29 tows and no catch in 59 tows, and 27 tows had missing

³A FORTRAN program to form the matrix and a SAS Institute, Inc. (1988) program to compute the group averages are available upon request.

information on the weight of a nonprohibited species. We included an additional 390 tows with missing weights for Pacific salmon and Pacific halibut. These catches may have slightly overestimated weights for the selected species because the catch weights included the prohibited species but the sample weights did not.

Assemblage Definition

We derived six consistent assemblages based on the three methods of analysis (Fig. 1 and 2). Two of the assemblages were dominated by single species, SHR and the widow rockfish assemblage (WID) (Fig. 2). The NSM assemblage contained sanddab, English sole, sand sole, starry flounder, and petrale sole (Fig. 2). The BRF assemblage contained yellowtail rockfish, canary rockfish, yelloweye rockfish, lingcod, bocaccio, and sharpchin rockfish. The DWD assemblage was primarily Dover sole and sablefish. The deepwater rockfish assemblage (DWR) contained darkblotched rockfish, Pacific ocean perch, splitnose rockfish, yellowmouth rockfish, and sharpchin rockfish. Other species considered were associated with the assemblages, but to a lesser degree (Fig. 2).

We found strong agreement between many of the strategy designations and the assemblage designations, but there were also some differences (Table 1). The tows placed in the SHR, NSM, and BRF assemblages were almost entirely designated

the respectively named strategies, and the species associated with the assemblages were similar to the targeted species of those strategies. The DWD tows were mainly designated as SDWD, with associated species similar to the DWD targeted species, but also had a number of SNSM designations (Table 1). Two of the consistent assemblages were not in strong agreement with a strategy. WID was associated with widow rockfish and contained most of the tows designated SMID, but also had a substantial number of SBRF tows. DWR was associated with rockfish species found in relatively deep water and contained tows designated as mainly SBRF or SDWD.

The six consistent assemblages designated were the result of 82% agreement between the Bray-Curtis clusters and the TWINSpan clusters (Table 1) and had varying degrees of overlap on the DCA axes (Fig. 1 and 2). The DCA program derived four axes in order of decreasing correspondence between the catch and species scores (Table 2). The first axis appeared to represent a general separation of catches containing rockfish species from those containing flatfish species, but also separated the rockfish catches into the WID, BRF, and DWR assemblages (Fig. 1 and 2). The second axis separated SHR from the other assemblages, particularly from DWR, NSM, and DWD. The third axis served to separate NSM from DWR and, to a lesser extent, DWD from NSM and DWR. The fourth axis was not used, since it represented a separation of rockfish

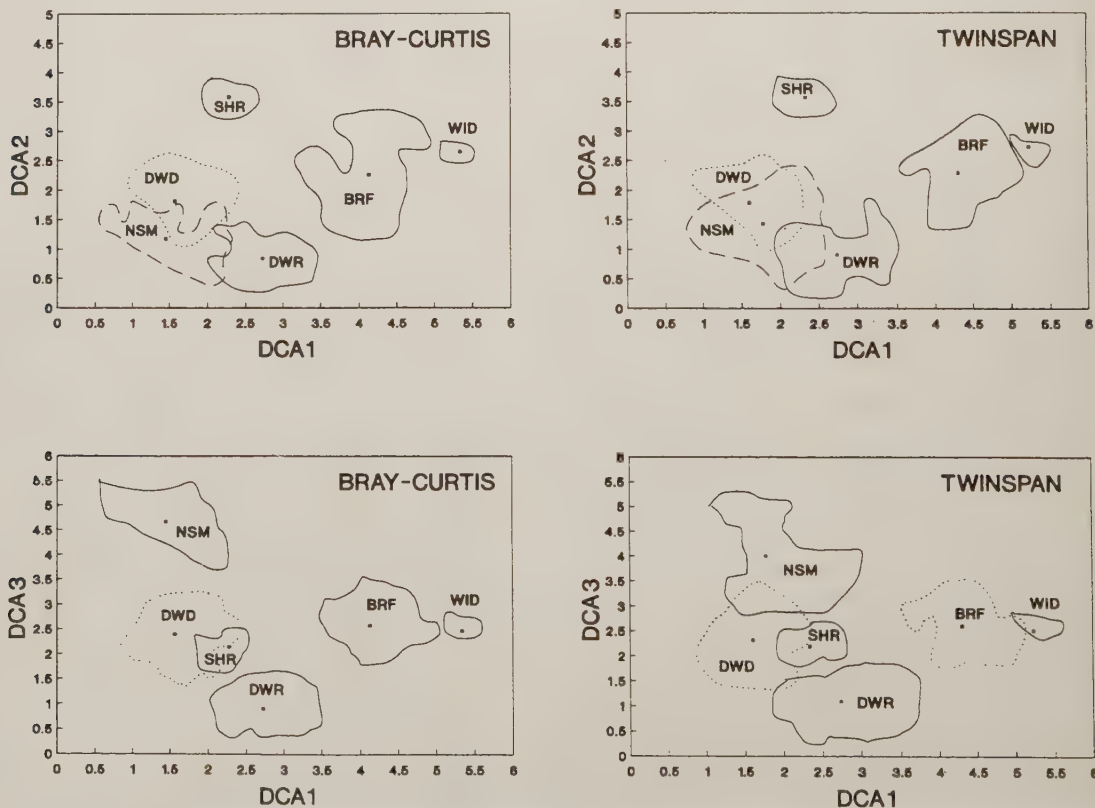


FIG. 1. Consistency of catch separations as demonstrated by the concentration of DCA catch scores for the Bray-Curtis clusters and TWINSpan clusters. The mean catch scores for the clusters are designated by a dot, while the outlines enclose 75% of the hauls in the cluster closest to the mean. The means are labeled to show the assemblage names assigned the respective clusters.

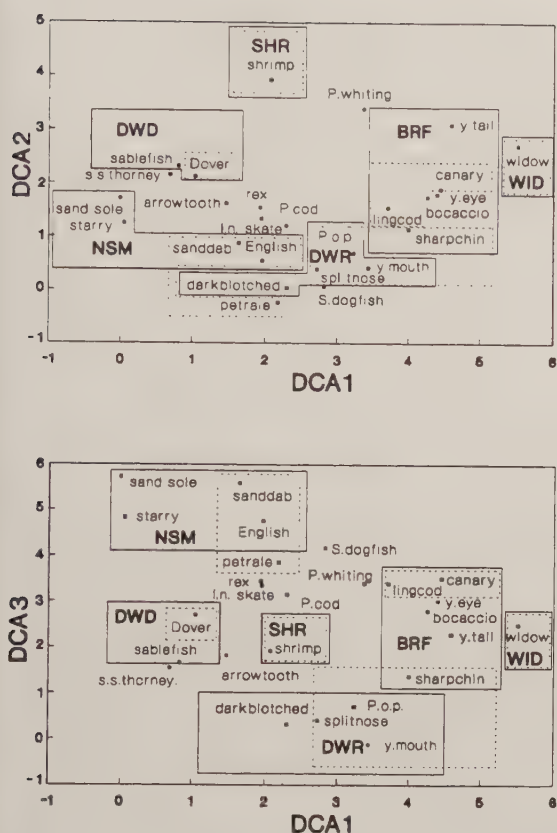


FIG. 2. Consistency in species associated with the catch clusters labeled by assemblage name. Species scores are designated by dots and labeled with species names. Dotted boxes enclose the indicator species of the TWINSpan clusters and solid boxes enclose the species associated with the Bray-Curtis clusters. Species selected for Bray-Curtis were those averaging >20% by weight in the catches and/or >4 times the average weight.

species inconsistent with the TWINSpan separation of species. The Bray-Curtis clustering tended to provide better separations on the DCA axes, particularly in separating DWD from NSM (Fig. 1).

Nine Bray-Curtis clusters were required to derive different groups at opposite ends of DCA axes 1–3 (Fig. 3). To achieve consistency with the clustering species associations, three Bray-Curtis clusters were combined to form BRF (Fig. 3). These clusters were associated with yellowtail rockfish, canary rockfish, or sharpchin rockfish. There was one inconsistent assemblage, named DOG because it was associated with spiny dogfish. It was primarily part of the TWINSpan DWD, but could not be included in the Bray-Curtis DWD without first combining DWR with DWD, and DWR was associated with an extreme of DCA axis 3 (Fig. 1 and 2). The species associations with the consistent Bray-Curtis assemblages, which were the basis of the outlines in Fig. 2, are shown in Table 3.

TWINSpan showed different clusters at opposite ends of the first three DCA axes after four divisions, resulting in 15 groups (Fig. 4). WID was not divided in the first division, since it included less than 1% of the catches. Many of the clusters

were recombined to be consistent with the other methods of analysis (Fig. 4). One of the four clusters combined to form NSM could be considered a transition cluster. It was intermediate in the separation of NSM and DWD on DCA axis 3, was placed primarily in the Bray-Curtis DWD, and was associated with sablefish, arrowtooth flounder, and Dover sole, along with petrale sole and sanddab. The species associations with the consistent TWINSpan assemblages, which were outlined in Fig. 2, are shown in detail in Table 4.

Discussion

Our results suggest that widow rockfish and smooth pink shrimp may be managed as separate species, but the other species could be managed as part of assemblages. As of October 1990, trip limit restrictions were in effect for two multispecies assemblages: a *Sebastes* complex (all rockfish except widow rockfish, Pacific ocean perch, thornyheads, and shortbelly rockfish (*Sebastes jordani*)) and a deepwater complex, including sablefish, yellowtail to 20–30% of the *Sebastes* complex, and Pacific ocean perch to 20% of all fish onboard within a given range of weights. Our findings agreed with use of the deepwater complex: Dover sole and sablefish were highly associated with our DWD assemblage, and thornyheads had the next closest association (Fig. 2; Table 3). In addition, sablefish averaged close to 25% by weight in the DWD catches (Table 3). We determined that the *Sebastes* complex could be divided into two assemblages, DWR and BRF, with Pacific ocean perch approximately 20% of DWR and yellowtail rockfish about 50% of BRF (Table 3). The possibility of setting separate trip limits for BRF and DWR could allow managers more flexibility in managing rockfish in the future.

To be useful to managers and modelers, the assemblages we defined should be persistent over time. The assemblages could change if the species mixes available to the fishermen change or the fishermen change the strategies they use to catch the species. The species available could change as a result of environmental changes or harvesting pressures. Strategies employed may change based on market prices, regulations, or new technology.

Although monitoring the fishery over time using our same methodology would be desirable to examine persistence of the assemblages, comparison of our study with other trawl studies conducted in the same area does indicate some persistence which is independent of methodology. Assemblages were defined previously with various methods of data analysis, using data collected with a variety of strategies, from time periods before, during, and after our data base. In spite of this, some consistencies were evident between our assemblages and those defined by other authors. A species association similar to our NSM was designated by Alverson (1953), Day and Percy (1968), Percy (1978), Gabriel and Tyler (1980), and Tyler et al. (1984). Prior studies determined a deepwater assemblage, although the DWR and DWD assemblages were often combined and a separate DWR was never distinguished. Alverson (1953), Hitz and Alverson (1963), Gabriel and Tyler (1980), and K. L. Weinberg (unpubl. data) defined species associations and assemblages using a combination of DWD and DWR species. Percy et al. (1982) determined a sablefish, Dover sole, and thornyhead cluster when investigating deepwater areas. Rickey and Lai (1990) analyzed only four species in defining a deepwater complex, but determined that Dover sole and

TABLE 1. Number of tows in strategies designated by observers and in assemblages determined by Bray-Curtis catch clusters, TWINSpan catch clusters, and both, designated as catching the same assemblage by both methods of clustering (tows that were inconsistent were not included).

	Designated strategy					Total
	SNSM	SDWD	SSHR	SBRF	SMID	
Bray-Curtis						
NSM	101	1	0	5	0	107
DWD	148	439	0	29	2	618
DWR	0	33	2	77	0	112
SHR	0	0	217	0	0	217
BRF	4	4	2	172	2	184
WID	0	0	0	25	24	49
DOG	8	13	1	17	0	39
TWINSpan						
NSM	192	4	6	8	0	210
DWD	73	455	3	44	0	575
DWR	0	33	1	98	0	132
SHR	0	0	211	4	7	222
BRF	1	0	2	162	2	167
WID	0	0	0	19	26	45
Both						
NSM	100	1	0	4	0	105
DWD	63	428	1	17	0	509
DWR	0	25	0	72	0	97
SHR	0	0	209	0	0	209
BRF	0	0	1	140	2	143
WID	0	0	0	15	24	39

TABLE 2. DCA species scores on axes 1-4, where scores are 100 times the units and closely related species have similar scores. Eigenvalues (EIG) represent the amount of correspondence between the species scores and the sample scores for that axis. DCA species axes are plotted in Fig. 2.

DCA1 (EIG = 0.901)		DCA2 (EIG = 0.718)		DCA3 (EIG = 0.525)		DCA4 (EIG = 0.358)	
Widow rockfish	551	Smooth pink shrimp	392	Sand sole	572	Canary rockfish	344
Yellowtail rockfish	460	Pacific whiting	339	Sanddab	559	Bocaccio	314
Canary rockfish	446	Yellowtail rockfish	310	Starry flounder	483	Yelloweye rockfish	306
Yelloweye rockfish	441	Widow rockfish	271	English sole	475	Darkblotched rockfish	277
Bocaccio	427	Sablefish	232	Spiny dogfish	417	Smooth pink shrimp	273
Sharpchin rockfish	400	Shortspine thornyhead	215	Petrale sole	385	Sand sole	272
Lingcod	370	Dover sole	212	Canary rockfish	351	Splitnose rockfish	265
Yellowmouth rockfish	343	Canary rockfish	190	Rex sole	344	Starry flounder	261
Pacific whiting	336	Yelloweye rockfish	180	Pacific whiting	340	Pacific ocean perch	232
Pacific ocean perch	323	Bocaccio	175	Lingcod	340	Yellowmouth rockfish	225
Spiny dogfish	282	Sand sole	171	Longnose skate	334	Sablefish	197
Splitnose rockfish	272	Arrowtooth flounder	162	Pacific cod	315	Shortspine thornyhead	187
Darkblotched rockfish	230	Lingcod	155	Yelloweye rockfish	302	Arrowtooth flounder	180
Pacific cod	229	Rex sole	155	Bocaccio	280	Widow rockfish	161
Petrale sole	218	Longnose skate	134	Dover sole	270	Lingcod	147
Smooth pink shrimp	207	Starry flounder	125	Widow rockfish	249	Sanddab	135
English sole	196	Pacific cod	121	Yellowtail rockfish	228	English sole	131
Longnose skate	195	Sharpchin rockfish	115	Smooth pink shrimp	192	Pacific whiting	91
Rex sole	193	Sanddab	88	Arrowtooth flounder	182	Dover sole	91
Sanddab	164	Pacific ocean perch	70	Sablefish	166	Spiny dogfish	78
Arrowtooth flounder	147	English sole	55	Shortspine thornyhead	154	Longnose skate	73
Dover sole	104	Yellowmouth rockfish	43	Sharpchin rockfish	137	Rex sole	59
Sablefish	81	Splitnose rockfish	40	Pacific ocean perch	70	Petrale sole	59
Shortspine thornyhead	70	Spiny dogfish	7	Splitnose rockfish	40	Pacific cod	54
Starry flounder	5	Darkblotched rockfish	4	Darkblotched rockfish	31	Sharpchin rockfish	25
Sand sole	-1	Petrale sole	-23	Yellowmouth rockfish	-12	Yellowtail rockfish	0

sablefish had the strongest association, followed by thornyheads and then arrowtooth flounder. One study defined an assemblage similar to BRF. K. L. Weinberg (unpubl. data) analyzed Scorpaenidae only and described an assemblage which

was associated with yellowtail and canary rockfishes.

Differences that did exist between the assemblages we defined and those defined previously were primarily a result of different placement of the boundaries separating the assem-

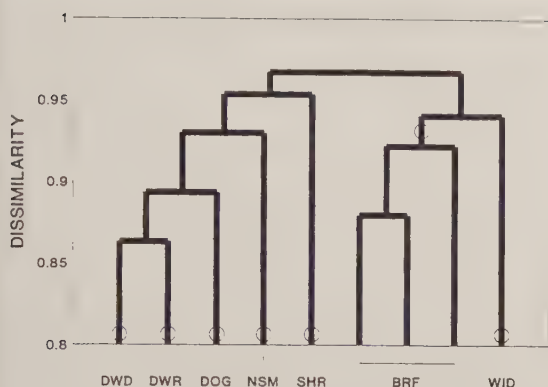


FIG. 3. Dendrogram of Bray-Curtis cluster combinations at increasing levels of dissimilarity. Level of dissimilarity selected in determining labeled assemblages is indicated by a circle.

blages. Not only were DWD and DWR often combined, but some studies determined additional assemblages which could be considered intermediate between our assemblages. An assemblage intermediate between NSM and DWD was described by Hitz and Alverson (1963), Day and Pearcy (1968), Pearcy (1978), and Tyler et al. (1984), between DWR and BRF by Gabriel and Tyler (1980), and between BRF and WID by K. L. Weinberg (unpubl. data). The one major difference

between our assemblages and those defined earlier which could not be attributed to differences in boundary placement was Gabriel and Tyler's (1980) definition of an assemblage which included Dover sole and Pacific whiting with canary rockfish. We did not find that those three species had any close association.

Differences among the assemblage definitions could result from many factors. It is possible that the location of the boundaries between assemblages depended on the method of data analysis employed. The previous studies generally used one or two types of analysis and stressed selection of assemblages with hauls made in the same depth range or area. For instance, we could have selected levels in the clustering that combined DWR and DWD, and may have done so if we had not considered the DCA axes separation of the two assemblages. Differences could also result from variations in the data. As stated previously, logbook and research data may not accurately reflect the commercial catch. The targeting and strategies used by commercial fishermen may have resulted in distinctions between assemblages which were not present in research catches. The research cruises were conducted using more restrictive time periods, bottom depths, and gear types than used by the commercial fishery. The studies that combined DWR and DWD were all based on research cruise data. The inclusion of discarded fish in the observer data versus the logbook data could also have affected the boundaries between assemblages. It is also possible that observer coverage of the commercial fleet was not representative of the total commercial effort. Another factor that may have caused the differences could be changes in the relative

TABLE 3. Species associations with Bray-Curtis catch clusters designated by assemblage name. Two indices of species associations are shown: %, average percent by weight in the hauls; $\bar{x}$ ratio of average weight in the assemblage catches to average weight caught for that species overall (where 4 = greater than or equal to 4 times the average, 3 = 2-4 times the average, 2 = average to 2 times, 1 = 0 to below average, and 0 = none).

Species	Assemblage													
	DWD		DWR		DOG		NSM		SHR		BRF		WID	
	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$
Dover sole	27	2	3	1	7	1	2	1	<1	1	<1	1	<1	1
Sablefish	21	2	5	1	3	1	<1	1	1	1	<1	1	<1	1
Shortspine thornyhead	7	3	2	1	1	1	0	0	<1	1	<1	1	<1	1
Arrowtooth flounder	11	2	2	1	5	2	<1	1	1	1	<1	1	0	0
Pacific ocean perch	3	1	21	4	1	1	<1	1	<1	1	1	1	<1	2
Darkblotched rockfish	3	1	31	4	2	1	0	0	<1	1	<1	1	<1	1
Yellowmouth rockfish	<1	1	14	4	<1	1	0	0	<1	1	1	1	<1	1
Splitnose rockfish	1	1	9	4	<1	2	0	0	<1	1	<1	1	0	0
Spiny dogfish	2	1	<1	1	62	4	<1	1	<1	1	<1	1	<1	1
Petrale sole	5	2	<1	1	4	3	10	2	<1	1	<1	1	<1	1
Sanddab	<1	0	0	0	<1	1	25	4	<1	1	<1	1	0	0
English sole	1	2	<1	1	<1	2	22	4	<1	1	<1	1	0	0
Sand sole	<1	1	0	0	0	0	18	4	0	0	0	0	0	0
Starry flounder	<1	1	0	0	0	0	2	4	0	0	0	0	0	0
Longnose skate	3	2	<1	1	1	2	6	2	<1	1	<1	1	<1	1
Rex sole	4	2	<1	1	2	2	6	2	1	1	<1	1	<1	1
Pacific whiting	7	1	3	1	2	1	6	1	12	1	1	1	2	1
Smooth pink shrimp	<1	1	0	0	0	0	0	0	78	4	<1	1	0	0
Pacific cod	1	2	<1	1	<1	1	<1	1	<1	1	<1	1	<1	1
Lingcod	1	1	<1	1	2	3	1	1	<1	1	7	4	<1	1
Yellowtail rockfish	<1	1	<1	1	2	1	<1	1	2	1	49	4	2	2
Canary rockfish	<1	1	<1	1	<1	1	<1	1	<1	1	18	4	1	3
Sharpchin rockfish	<1	1	4	3	2	3	<1	1	<1	1	9	4	<1	2
Bocaccio	<1	1	<1	1	<1	1	<1	1	<1	1	3	4	<1	3
Yelloweye rockfish	<1	1	<1	1	<1	1	<1	1	0	0	2	4	<1	2
Widow rockfish	<1	1	3	1	<1	1	0	0	<1	1	1	1	92	4

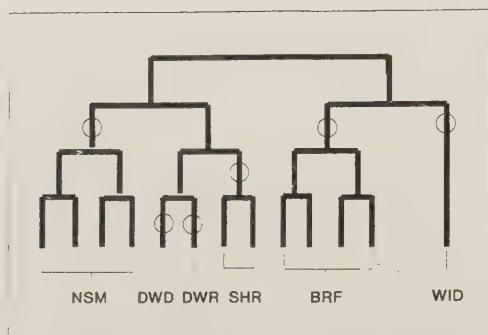


FIG. 4. Dendrogram of TWINSpan haul cluster divisions at progressive separations. Level of separation selected in determining labeled assemblages is indicated by a circle.

amounts of the species within assemblages over time. Most of the other studies used data collected prior to our data base. Further study is needed to determine the actual reasons for dissimilarities noted between our assemblage definitions and those defined previously.

Some of the strategies defined by Pikitch et al. (1988) based on gear, water depth, and targeted species appeared accurate and effective, allowing prediction of the assemblages caught, but some modifications appeared necessary (Table 1). Comparison of strategy and assemblage designations indicated that the use of shrimp gear was adequate to predict the catch of SHR, and fishermen using midwater gear nearly always caught WID. NSM was caught with mud gear in less than 183 m, but some DWD was also caught in the shallower water. Mud gear used in water greater than 183 m caught DWR as well as DWD. BRF was caught primarily with roller gear, but that gear was also used to catch WID and DWR. The strategies need modification because either targeting was ineffective or samplers, constrained to the five defined strategies, designated strategies based more on the gear and depth than on targeted species. The similarities that were present between the designated strategies and the assemblages imply that targeting was effective on certain assemblages, particularly SHR and WID, and that the strategies generally remained stable over time.

Comparing the results of the three methods of analysis not only led to assemblages relatively independent of method used,

but also allowed us to determine the hierarchical levels to select in the clusterings. A common problem in using hierarchical clustering is determining the level(s) on the dendrogram at which to select the clusters (Boesch 1977). The DCA ordination axes pointed out the major sources of variation in the data which should be included in the selected clusters. By combining or dividing clusters until the groups included the DCA axis separations and were consistent between the two types of clustering, we utilized the strengths in the different clustering methods. Consistent groups formed by the two clustering methods balanced the disadvantages and advantages of each method. TWINSpan started with the data base as a whole and therefore used the maximum amount of information in determining the major breaks in the data, making it a more robust technique than group average fusion (Gauch and Whittaker 1981). It also used the original data rather than a secondary dissimilarity matrix and integrated the classifications of both catches and species (Gauch 1980). A disadvantage is that it was biased towards forming subdivisions of nearly equal size during each division (Boesch 1977). It also had the disadvantage that each split was not treated totally hierarchically, since each cluster split at each level of the dendrogram. Further analysis to determine average ordination distances between clusters would have been required to achieve a fully hierarchical dendrogram (Gauch and Whittaker 1981). Defining species based on abundance levels in TWINSpan allowed consideration of both scarce and dominant species, but had the disadvantage that different abundances of a species were treated as separate species, with arbitrary cutoff values. The Bray-Curtis index with group average fusion clustering utilized the range of abundances of the species, but placed emphasis on dominant species and large hauls (Clifford and Stephenson 1975). Comparing the clusters formed by the two different methods allowed us to better determine the hierarchy of the TWINSpan splittings, and balanced the influence of dominant and scarce species.

Conclusions and Recommendations

Six major assemblages of species could be used by managers and modelers to develop management plans for the trawl fishery operating off the Oregon and Washington coasts. Two of the assemblages were dominated by single species, widow rockfish or smooth pink shrimp. The other four included a deepwater Dover assemblage, a deepwater rockfish assemblage, a bottom rockfish assemblage, and a nearshore mixed-species assem-

TABLE 4. Species associations with TWINSpan haul clusters designated by assemblage name. Species associations shown are the inclusive weight categories (kilograms per haul) of the indicator species as determined by TWINSpan.

Species	Assemblage					
	DWD	DWR	NSM	SHR	BRF	WID
Dover sole	15-933					
Pacific ocean perch		15-126				
Yellowmouth rockfish		>0-126				
Splitnose rockfish		>0-15				
Sharpchin rockfish		>0-15				
Petrale sole			>0-15			
Sanddab			15-126			
English sole			>0-126			
Smooth pink shrimp				15-126		
Lingcod					>0-15	
Canary rockfish					>0-126	
Widow rockfish						>15

blage. The separation of the deepwater rockfish assemblage from the bottom rockfish assemblage has not been previously used in setting trip limits, and the separation of a deepwater rockfish assemblage from deepwater Dover was not previously designated quantitatively.

Although we could not unambiguously determine year-to-year persistence of the assemblages based on the limited number of years in our data base, comparison with past studies did indicate that there may be some persistence. There were overall similarities between our findings and assemblages defined previously based on logbook or research data collected in other periods. It is possible that the assemblages caught were based on relatively stable biological associations of the species, which limited the possible technological interactions.

Our results indicated that the strategies defined by Pikitch et al. (1988) need some modification to accurately predict the assemblages caught. These modifications may include designating a separate deepwater rockfish strategy, a widow strategy using roller gear as well as midwater gear, and reducing the depth criteria separating the nearshore mixed-species and deepwater Dover sole strategies.

The method we used to determine the assemblages using consistencies from three methods of analysis could be applied to other data bases. An advantage of our method is that it allows relatively objective determination of assemblages based solely on species abundances in samples. Our method allows definition of groups which reflect the major sources of variation in the data, without requiring knowledge of the factors that cause the variation.

Future studies could include further assessment of the similarities and differences between logbook, research, and observer data. We found general consistencies in assemblages defined from the different types of data, but there was variation in the placement of the boundaries between assemblages. Differences may be more evident or conclusive if comparisons are based on data collected in the same years and analyzed using the same methodology.

Comparison of targeted species with species caught and assessment of the species discarded could be useful. It would help determine if the modifications in the strategies described by Pikitch et al. (1988) are required because targeting was ineffective or because the strategies did not accurately define the behavior of the fishermen during the study.

It would be valuable to define strategies quantitatively for each of the assemblages, based solely on the operational decisions the fishermen make, and without relying on knowledge of the targeted species. It could provide necessary modifications to the strategies as well as aid managers and fishermen in determining how to control the catch of the six assemblages defined in this paper.

Acknowledgements

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Optimal course by dolphins for detection avoidance

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One of the assumptions of line transect sampling is that movement of animals being counted is not in response to the approaching vessel before the animals are detected (Burnham et al. 1980). By observing from a helicopter the reaction of dolphins to an approaching survey vessel, Au and Perryman (1982) and Hewitt (1985) demonstrated that dolphin schools can detect the approach and maneuver to attempt to avoid detection. Because it may be that dolphin exhibit forms of optimal behavior (Au and Weihs 1980), it is of interest to determine whether there is a direction the

dolphin should take that maximizes their distance to the vessel at the point of closest approach and, if there is such a direction, to determine whether dolphin use it. If this is so, this may be the way of determining through aerial means when dolphin first react to an approaching vessel and whether it is after they are detected by a shipboard observer.

Since the advent of purse-seine fishing in the eastern tropical Pacific in 1959, dolphin that associate with yellowfin tuna (i.e., primarily *Stenella attenuata*, *S. longirostris*, and *Delphinus delphis*) are chased,

caught in nets, and sometimes drowned (Perrin 1968, 1969). Stuntz and Perrin (1979) reported that these species of dolphin are more difficult to capture in areas where purse-seine-vessel fishing effort has been greatest, implying that evasive behavior may be learned. It has also been reported by Au and Perryman (1982) that evasive maneuvers by dolphin upon approach of a vessel sometimes begin at a distance that is approximately the shipboard observer's horizon. Because the visual horizon of even a leaping dolphin is shorter than that of a shipboard observer, it is likely that they are reacting to the vessel sound. It is therefore plausible that by experiencing repeatedly the approach of such vessels, dolphin not only have learned to evade but do so optimally by choosing through trial and error the direction of escape, if it exists, in which the noise amplitude increases the least. Because the attenuation of sound is proportional to the distance transversed by it, escaping from a sound source in the direction where the amplitude increases the least is the same direction that maximizes the distance between a uniformly-moving source and receiver at the point of closest approach.

Here, we formulate the following problem: Upon detecting the approach of a vessel, a dolphin attempts to avoid detection by retreating. If the velocity of the vessel is V_B and that of the dolphin is V_D , is there a direction in which a dolphin can escape to maximize its distance from the vessel at the point of closest approach (Fig. 1)? And if so, what direction is it? We will show that there is such a direction: If α is the angle between V_B and V_D , the angle $\alpha = \arccos(V_D/V_B)$, where V_B and V_D are, respectively, the speeds of the vessel and the dolphin, will maximize the distance

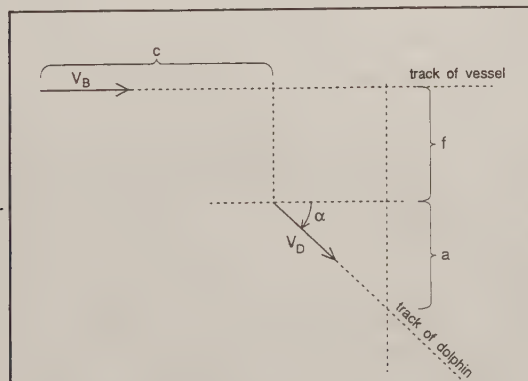


Figure 1

The vessel traveling at speed V_B and the dolphin traveling at V_D as seen in the stationary frame of reference. The direction α is the one chosen by the dolphin. Distance f is the perpendicular distance between the initial position of the dolphin and the projected path of the vessel, while $a+f$ is the distance between vessel and dolphin when the dolphin is abeam.

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between vessel and dolphin at the point of closest approach.

Finally, to ease the task of data analysis by whoever makes the necessary observations, we have derived the expressions that relate dolphin speed and direction to their range and bearing from the vessel. In a cartesian coordinate system let V_x and V_y be, respectively, the x and y components of the dolphin velocity minus, respectively, the x and y components of the vessel velocity. Both V_x and V_y are constructed using range and bearing measurements of the dolphin from the vessel. Then $V_D = [(V_x + V_B)^2 + V_y^2]^{1/2}$ and $\alpha = \arctan [V_y / (V_x + V_B)]$.

Problem solution

As stated in the formulation above, the problem makes sense only for the case $V_D \leq V_B$. With reference to Figure 2, to maximize the distance between vessel and dolphin at the point of closest approach, we must find the maximum value of $r_{\min}$ with respect to angle $0 \leq \alpha \leq \pi$.

For the purpose of the following exposition, we define initial position to be that position of the vessel (or the dolphin) at the time when the dolphin detects the approaching vessel and begins evasion. Initial time is the time corresponding to the initial position.

In Figure 2, at the point of closest approach the distance between vessel and dolphin is given by

$$r_{\min} = (a + f) \cos \beta, \quad (1)$$

where $0 \leq \beta \leq \pi/2$, f is the perpendicular distance between the initial position of the dolphin and the projected path of the vessel, and $(a + f)$ is the distance between vessel and dolphin when the dolphin is abeam. The vector diagram of Figure 2 shows that the apparent track of the dolphin as seen from the vessel is a function of α , the direction of escape of the dolphin. Therefore, to solve the problem as posed, we must find the extreme value of Eq. (1) with respect to angle α .

By computing the derivative with respect to α of Eq. (1), we find that $r_{\min}$ is rendered an extreme value when

$$\frac{dr_{\min}}{d\alpha} = \cos \beta \frac{da}{d\alpha} - (a + f) \sin \beta \frac{d\beta}{d\alpha} \quad (2)$$

vanishes. Depending on the functional dependence of a and β on α , an equation of the form of Eq. (2), could vanish either term by term or by cancellation of the terms. For the former case, each term could vanish trivially (i.e., a and β are independent of α), or non-trivially (i.e., both a and β are rendered extreme values

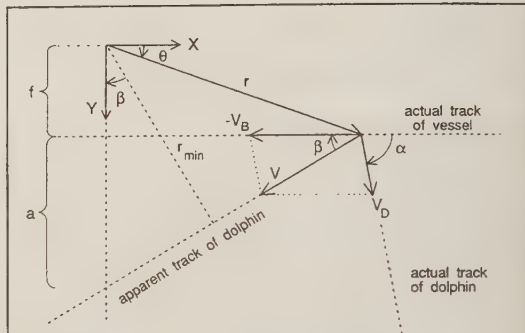


Figure 2

The apparent motion of the dolphin as seen in the moving frame of reference of the vessel. The apparent velocity V of the dolphin is the resultant of the vector addition of $-V_B$ and V_D . Distance f is the perpendicular distance between the initial position of the dolphin and the projected path of the vessel, while $a + f$ is the distance between vessel and dolphin when the dolphin is abeam.

with respect to α simultaneously).

In Figure 1, c is the distance along the projected path of the vessel between the vessel's initial position and the point that is abeam of the dolphin's initial position. Let t_c be the time it takes the vessel to transverse distance c , and t that time from the initial time until the vessel has the dolphin abeam. From the application of the Pythagorean Theorem we can deduce

$$(V_D t)^2 = a^2 + [V_B(t - t_c)]^2. \quad (3)$$

Because

$$a = V_D t \sin \alpha, \quad (4)$$

it can then be shown by substitution of Eq. (4) into Eq. (3) that

$$t = \frac{t_c}{1 - (V_D/V_B) \cos \alpha}. \quad (5)$$

By substituting Eq. (5) into Eq. (4), we find that as a function of α , a is given by

$$a = \frac{V_D t_c \sin \alpha}{1 - (V_D/V_B) \cos \alpha}. \quad (6)$$

Because at least a is a function of α , we can conclude that in general Eq. (2) does not vanish trivially. However, β is also a function of α as can be deduced by the application of the Law of Sines to Figure 2:

$$\beta = \arctan \left[\left(\frac{V_D}{V_B} \right) \frac{\sin \alpha}{1 - (V_D/V_B) \cos \alpha} \right]. \quad (7)$$

Next we investigate whether Eq. (2) vanishes non-trivially. Computing the derivative with respect to α of Eq. (6), we get

$$\frac{da}{d\alpha} = \frac{V_D t_c [\cos \alpha - (V_D/V_B)]}{[1 - (V_D/V_B) \cos \alpha]^2}, \quad (8)$$

which vanishes only if

$$\alpha = \arccos \left(\frac{V_D}{V_B} \right) = \alpha_0. \quad (9)$$

Noting the similarity between a and β given respectively in Eq. (6) and (7), we can easily and simply express one in terms of the other. Writing

$$\beta = \arctan \left[\frac{a}{V_B t_c} \right], \quad (10)$$

the derivative of β with respect to α is given by

$$\frac{d\beta}{d\alpha} = \frac{\cos^2 \beta}{V_B t_c} \frac{da}{d\alpha}. \quad (11)$$

Substituting into Eq. (2) the equivalence of Eq. (11), we find that

$$\frac{dr_{\min}}{d\alpha} = \cos \beta \left[1 - \frac{(a+f) \sin \beta \cos \beta}{V_B t_c} \right] \frac{da}{d\alpha}, \quad (12)$$

which allows us to conclude that $r_{\min}$ is extreme at the point $\alpha = \alpha_0$ because, as we found in Eq. (8), a is extreme at that point. However, as can be appreciated in Eq. (12), there may be other points where $r_{\min}$ is extreme. We now investigate whether $r_{\min}$ is extreme for values of α other than α_0 .

Other extreme values of $r_{\min}$ may be attained if

$$\cos \beta = 0 \quad (13)$$

or

$$(a+f) \sin \beta \cos \beta = V_B t_c \quad (14)$$

are physically realizable. Eq. (13) is satisfied for $\beta = n\pi/2$ ($n=1, 3, 5, \dots$), and of these only $\beta = \pi/2$ concerns us. It corresponds to the upper limit of the physically realizable range of $0 \leq \beta \leq \pi/2$, and represents the uninteresting case $V_D = V_B$ (i.e., $\alpha_0 = 0$) which is the trivial special case of this problem: $r_{\min}$ is rendered constant when $V_D = V_B$ (i.e., the dolphin swims with

the same velocity as the vessel), so the vanishing of Eq. (2) is trivially satisfied.

In Eq. (14) let $f=0$. This limit will not diminish the generality of the solution. The direction a dolphin should take to maximize its distance to the vessel at the point of closest approach will not depend on how close the dolphin is initially to the projected path of the vessel. So without loss of generality we investigate if there is a physically realizable angle β such that

$$a \sin \beta \cos \beta = V_B t_c \quad (15)$$

is satisfied. With the result from Eq. (10) and the identity $\tan \beta = \sin \beta \cos^{-1} \beta$, Eq. (15) can be expressed as the condition $\sin \beta = \pm 1$ which is satisfied by the same uninteresting case that satisfies Eq. (13). Therefore, we can conclude that the nontrivial extreme value attained by $r_{\min}$ at $\alpha = \alpha_0$ is unique in the interval $0 \leq \alpha \leq \pi$.

We only have left to show that the extreme value attained by $r_{\min}$ at $\alpha = \alpha_0$ is a maximum. Let a_0 and β_0 be the respective values of a and β at $\alpha = \alpha_0$. The second derivative of $r_{\min}$ with respect to α evaluated at $\alpha = \alpha_0$ is given by

$$\frac{d^2 r_{\min}}{d\alpha^2} \Big|_{\alpha_0} = \cos \beta_0 \left[1 - \frac{a_0 \sin \beta_0 \cos \beta_0}{V_B t_c} \right] \frac{d^2 a}{d\alpha^2} \Big|_{\alpha_0}. \quad (16)$$

Because the second derivative of a with respect to α evaluated at $\alpha = \alpha_0$ is

$$\frac{d^2 a}{d\alpha^2} \Big|_{\alpha_0} = \frac{-V_D t_c}{[1 - (V_D/V_B)^2]^{3/2}} < 0, \quad (17)$$

to determine whether Eq. (16) is negative we must show that

$$a_0 \sin \beta \cos \beta_0 < V_B t_c. \quad (18)$$

We have shown already that Eq. (15) can only be satisfied for an angle $\beta = \pi/2$. Then Eq. (18) is satisfied for $0 \leq \beta < \pi/2$. We have seen already that $\beta = \pi/2$ when $\alpha = 0$, so $da/d\alpha = 0$ at that point also. Therefore, we can also conclude that the nontrivial extreme value achieved by $r_{\min}$ at $\alpha = \alpha_0$, unique in the interval $0 \leq \alpha \leq \pi$, is a maximum. Because Eq. (2) vanishes term by term, the same result is achieved by finding the extreme value with respect to α of either β or a .

In conclusion, a dolphin escaping at speed V_D at an angle α relative to the velocity V_B of an approaching vessel will maximize its distance to the vessel at the point of closest approach if $\alpha = \arccos(V_D/V_B)$.

Determination of dolphin velocity from range and bearing measurements

In this section we relate the dolphin velocity to practical *in situ* measurements. We will derive a relationship between dolphin speed and direction to its range $0 \leq r < \infty$ and bearing $0 \leq \theta \leq 2\pi$ from the vessel that triggers the dolphin to flight.

For the times $\{t_i: i = 1, 2, \dots, n\}$ we perform the corresponding measurements $\{r_i, \theta_i: i = 1, 2, \dots, n\}$. It is not necessary that the measurements be made from the vessel, but with reference to it (e.g., aerial measurements). However, it is necessary that there be no other vessel in the vicinity that perturbs the measurements by reaction of the dolphin to its presence.

The measurements of range and bearing of the dolphin from the vessel are equivalent to the cylindrical coordinates of the dolphin with respect to the moving frame of reference of the vessel. The cartesian coordinates $-\infty < x < \infty$ and $-\infty < y < \infty$ with respect to the same frame of reference are determined from

$$x = r \cos \theta \text{ and } y = r \sin \theta. \quad (19)$$

Let Δx , Δy , and Δt be, respectively, the increments of the variables x , y , and t . For each of the $(n-1)$ consecutive intervals, we can compute the average speeds in the x and y directions by

$$V_x = \frac{\Delta x}{\Delta t} \text{ and } V_y = \frac{\Delta y}{\Delta t}. \quad (20)$$

These are the components of the dolphins' apparent velocity V in the frame of the moving vessel (Fig. 2). We can express the dolphin velocity in the moving frame as a function of its speed and direction in the stationary frame by

$$V_x = V_D \cos \alpha - V_B \text{ and } V_y = V_D \sin \alpha, \quad (21)$$

which are a system of two coupled, nonlinear equations with V_D and α as unknowns. The solution to this set of equations is given by

$$V_D = \sqrt{V_x^2 + V_y^2}, \quad (22)$$

where we have chosen the positive root, and

$$\alpha = \arctan \left(\frac{V_y}{V_x + V_B} \right). \quad (23)$$

With these results we can compare the $(n-1)$ time-intervals the direction α taken by the dolphin given Eq. (23), with the optimal direction given in Eq. (9) computed from the result given Eq. (22).

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SEABIRD-FISHERIES INTERACTIONS: EVALUATION WITH DIMENSIONLESS RATIOS

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Abstract. Marine bird populations interact with fisheries in a variety of ways, with diverse outcomes. Evaluation of these outcomes requires a means of comparison across cases, and a means of identifying the relative importance of concomitant processes at relevant space and time scales. We describe a general quantitative framework that permits comparison of quantitative findings among studies of seabird-fisheries interactions. We then review the results of seabird-fisheries studies within this framework. We discuss the use of ad hoc ratios and dimensional analysis to make decisions about competing processes at relevant space and time scales.

INTRODUCTION

The diversity of interactions of marine bird populations with fisheries (Duffy and Schneider *in press*) includes provision of offal to birds, removal of predators that take the same prey as seabirds, reduction in seabird prey heavily fished by commercial fleets, use of seabirds to locate fish, use of seabirds as bait, near sinking of a fishing vessel by birds, fertilization of coastal waters with guano, reduction in fishery landings due to prior removal by seabirds, piracy by seabirds, and seabird mortality in nets. Outcomes range from positive through neutral to negative for both birds and humans. Examples of all 9 possible outcomes in a two way classification (positive, neutral, negative for birds) x

(positive, neutral, negative for humans) occur (Duffy and Schneider *in press*).

Effective seabird conservation depends upon accurately identifying the causes of negative outcomes. The problems that arise in identifying negative effects on marine birds arise in many wildlife management situations: the time and space scales of causes are unknown, the relative importance of concomitant processes is unknown, and the applicability of other cases to the problem at hand is unknown. In this paper we describe a comprehensive quantitative framework that addresses problems of scale, competing processes, and comparability of results from multiple studies. We show that the framework can be used to review and compare studies of seabird-fisheries interactions. We then demonstrate the use of dimensionless ratios to evaluate competing processes. Dimensionless ratios currently in use will be compared to those arising from dimensional analysis.

QUANTITATIVE FRAMEWORK

The interaction of seabirds, humans, and their marine prey is highly diverse, with elements of interference competition, scramble competition, predation, parasitism, and mutualism (Duffy and Schneider *in press*). These interactions occur primarily at the interface of two fluids, the atmosphere and the ocean, which are in constant motion. Thus, elements of fluid dynamics, ethology, and demography all contribute to changes in seabird populations, and are important in understanding seabird-fisheries interactions. These elements can be incorporated into a single quantitative framework (Schneider 1991) in which the rate of change in local abundance results from demographic, ethological, and fluid processes (Table 1). After commenting briefly on trends in the density and spatial

TABLE 1. Marine bird population interactions with fisheries equations relating state factor distributions to dynamic variables. The equations state, in measurable quantities, that local density changes $[\dot{Q}]$ of vessels, birds or nekton, result from the appearance of new vessels or animals $\dot{R}$, loss or death $\dot{D}$, divergence or convergence due to directed movements $\nabla_h \cdot \mathbf{u}$ relative to the surrounding fluid, and divergence or convergence due to passive drift in the atmosphere $\nabla_h \cdot \mathbf{u}_{Am}$ or in the ocean $\nabla_h \cdot \mathbf{u}_{Oc}$. The rate of change in density $[\dot{Q}]$ has the same dimensions ($\% \text{ time}^{-1}$) as the several dynamic terms on the right side of the equation. Terms are defined in greater detail in Appendix 1.

State factor	Distribution	Demography	Ethology	Fluid dynamics	
Fishing Vessels	$[\dot{Q}_V]$	$= \dot{R}_V - \dot{D}_V$	$- \nabla_h \cdot \mathbf{u}_V$	$- \nabla_h \cdot \mathbf{u}_{Am}$	$- \nabla_h \cdot \mathbf{u}_{Oc}$ (1)
Nekton	$[\dot{Q}_N]$	$= \dot{R}_N - \dot{D}_N$	$- \nabla_h \cdot \mathbf{u}_N$		$- \nabla_h \cdot \mathbf{u}_{Oc}$ (2)
Birds	$[\dot{Q}_B]$	$= \dot{R}_B - \dot{D}_B$	$- \nabla_h \cdot \mathbf{u}_B$	$- \nabla_h \cdot \mathbf{u}_{Am}$	$- \nabla_h \cdot \mathbf{u}_{Oc}$ (3)

dynamics of fishing vessels (Table 1, equation 1) and on general knowledge of the density and dynamics of nekton (Table 1, equation 2), we review briefly what is known about each of the terms in equation 3 (Table 1), which relates distribution ($[\dot{Q}_B]$) to the demographics ($\dot{Q} = \dot{R}_B - \dot{D}_B$) and kinematics ($\dot{A} = -\nabla_h \cdot u_B - \nabla_h \cdot u_{Am} - \nabla_h \cdot u_{Oc}$) of marine bird populations.

Demographics and spatial dynamics of fishing vessels

All of the dynamic terms in equation 1 (Table 1) have changed in the last century toward greater concentration of fishing effort, measured by $[\dot{Q}_V]$. Effort has increased under the combined action of technological advances, economic forces and political pressures (Cushing 1975). The number of new vessels has increased ($\dot{R}_V > 0$), a development permitted by advances in ship design, and driven by the economics of open fisheries, which distribute the cost of entry over all vessels, rather than placing it on the entrant (Gordon 1954). Vessel loss $\dot{D}_V$ has decreased due to advances in navigational technology and weather forecasting. Rate of convergence of fishing power $-\nabla_h \cdot u_V$ into limited areas of high fish abundance has increased through ever more effective use of information on ocean conditions and fish movements (Yudovich and Baral 1968). This trend is now being furthered with the use of larger-scale information from satellites. The development of fish-reducing plants in the early part of this century, followed by placement of these plants on ships in the 1930's (McEvoy 1986), contributed to the convergence of fishing power on highly mobile schooling organisms (notably clupeid fishes, squid, and krill), which are important prey of seabirds. Increases in vessel size and advances in ship design have reduced the influence of wind and currents $\nabla_h \cdot u_{Am} + \nabla_h \cdot u_{Oc}$ on fishing activities.

Population assessment of nekton

Quantitative knowledge of marine nekton (fish, squid, decapods, and euphausiids) decreases moving from left to right in equation 2 (Table 1). Much is known about spatial and temporal change in density; recruitment is the best studied process, mortality is less understood, and movements are least understood. One important negative finding is that recruitment ($\dot{R}_N$) in many nekton populations is unrelated to abundance $[Q_N]$ at the scale of the entire stock, except that $\dot{R}_N$ does decrease at very low values of $[Q_N]$ (Cushing 1975). With respect to management, another important finding is that demersal fish composed of multiple year classes can be managed (leaving aside economic and political pressures) by ignoring movements and recruitment, and concentrating instead on yield-per-recruit and the problem of growth overfishing (Gulland 1989). This strategy does not work with schooling pelagics because of their behavior (Csirke 1988), because of the greater concentration of production into fewer cohorts, and because of the tendency of fishing to reduce the number of cohorts in a population (Radovich 1981).

Rate of change in avian density

Information on avian density $[Q_B]$ at sea has increased rapidly in the last two decades. Despite the increase, knowledge of patterns of change in density at sea lags

considerably behind that for colonies. Seasonal changes at sea (Shuntov 1972, Powers 1983, Schneider et al. 1987) appear to be as large as those at colonies. Changes have been measured at the scale of 10^2 km or less. At this scale, changes are generally due to movements ($\hat{A}$), rather than demographic changes ($\hat{Q}$). Changes in avian density at this scale have been linked to release of offal from trawlers (Fisher 1952, Trukhin and Kosygin 1987, Abrams 1983), and the collapse of capelin stocks (Erikstad et al. 1990). The evidence for offal-related changes in distribution at this scale (Blake 1984) is not compelling (Furness et al. 1988) and other explanations are equally tenable (Brown 1970). At a much smaller scale, changes in density near trawlers are unquestionably due to the production of offal (Furness et al. 1988).

A number of studies have compared changes in density [$\hat{Q}_B$] measured at colonies with changes in fish density [$\hat{Q}_N$], which are estimated at the spatial scale of the stock, usually $> 10^2$ km, and often $> 10^3$ km. A relation has been reported in some cases (Duffy 1983a, Springer 1991) but not others (Bailey and Hislop 1978), or only at some locations within an area (Burger and Cooper 1984). At a still smaller scale (Monaghan and Zonfrillo 1986) the numbers of breeding terns in the Firth of Clyde was associated with an index of the abundance of larval herring. Cairns (1987) proposed that [$\hat{Q}_B$] was related to prey abundance only if prey abundance was low. This was corroborated at Røst, in Norway, where [$\hat{Q}_B$] = $-8\% \text{ yr}^{-1}$ in puffins (Anker-Nilsson and Lorentsen 1990) and $-3.3\% \text{ yr}^{-1}$ in murre (Vader et al. 1990) since the collapse of herring stocks. Further support comes from changes in diet associated with several local fishery failures in eastern Newfoundland (Montevecchi et al. 1987). The assumption implicit in these comparisons is that movements of breeding birds between colonies are negligible ($\hat{A} = 0$) and hence that observed change in abundance reflects demographic changes ($\hat{Q}$).

Avian recruitment

Most seabird research has focused on recruitment ($\hat{R}_B$) because this can be measured directly at the colony, either as number of chicks fledged, or as eggs produced, modified by mortality until fledging. Annual recruitment, defined in this way, varies considerably from place to place (Hunt et al. 1986). Annual recruitment also varies among species within colonies (Brown and Nettleship 1984, Springer 1991) and from year to year. Causes of temporal and spatial variation in $\hat{R}_B$ include pesticides (Anderson and Gress 1984), parasites (Duffy 1983b), weather, and prey availability (Furness 1984, Hislop and Harris 1985). The colony at Røst, in Norway, provides one of the clearest examples of the effects of prey availability on $\hat{R}_B$. Recruitment in puffins has been zero due to chick starvation (Lid 1981, Anker-Nilsson 1987) in nearly every year since the late 1960's when the herring stock collapsed from the interacting pressures of fishing and natural mortality (Jakobsen 1985, Rottingen 1985). A relation between recruitment and local fishing pressure also has been reported in the Shetland Islands (Monaghan et al. 1989) and the California Current before 1970 (Anderson and Gress 1984). Contradictory information (Springer 1991, Hatch et al. *in press*) precludes any firm conclusion about the role of fishing in suppressing kittiwake recruitment in the Bering Sea.

Avian mortality

Mortality rates ($\dot{D}_B$) of seabirds are on the order of 10% yr⁻¹ or less once birds begin breeding. Observations away from the colony (Bailey and Davenport 1972, Blake et al. 1984) suggest that this mortality may be episodic and highly localized, rather than occurring as a steady decay in numbers. One source of mortality is drowning in gill nets (Jones and DeGange 1988), especially among alcids (Carter and Sealy 1984, Piatt and Reddin 1984, Piatt et al. 1984, Vader et al. 1990). These mortalities are estimated as numbers killed (D), rather than rates ($\dot{D}$), because the source populations are unknown. In the North Pacific, for example, estimates of loss to salmon nets are on the order of 0.1 to 0.8 x 10⁶ per year (Ogi 1984, King 1984, DeGange et al. *in press*). Many of the murre in this total may come from the Aleutian Islands, and so net mortality may account for a substantial fraction of total mortality in these populations (King 1984). Murre losses to gill nets in California was stated to be large enough to affect local colonies (Jones and DeGange 1988). No rates were reported and the loss has now been regulated. In the southern Benguela Current, $[\dot{Q}_B] < 0$ for African penguins, while $\dot{R}_B > 0$. Wilson et al. (1988) hypothesize that $\dot{D}_B > \dot{R}_B$ during a period of high spatial overlap of purse seiners with juvenile penguins. A high ratio of $[\dot{Q}]$ to $\dot{R}_B$ in a colony of wandering albatross has been attributed to net mortality $\dot{D}_B$ (Weimerskirch and Jouventin 1987). Mortality due to fishing activity also occurs when birds are used for bait (Collins 1884), but no quantitative estimates are available for current fisheries. McIntosh (1903) suggested that direct mortality due to fishing activities may be large enough to offset competition with fisheries; i.e., that the ratio $\dot{D}_{B \rightarrow V} / (\dot{R}_{\max} - \dot{R}_{BIV})$ exceeds unity, where $\dot{R}_{BIV}$ denotes fledging rate in the presence of fishing vessels taking the same prey. Fishing could, in theory, decrease mortality $\dot{D}_B$ by releasing offal, especially for large bodied fish (Furness et al. 1988).

Avian movements

Little is known about avian movements relative to the surrounding fluid ($-\nabla_h \cdot \mathbf{u}_B$). Simultaneous observations of numbers and flight direction at a series of coastal points (Blomqvist and Peterz 1984) and tracking of individuals (Jouventin and Weimerskirch 1990), suggest that net movement results from behavioural interactions with the surrounding fluid ($\nabla_h \cdot \mathbf{u}_B = f(\nabla_h \cdot \mathbf{u}_{Am} + \nabla_h \cdot \mathbf{u}_{Oc})$). Winds ($\nabla_h \cdot \mathbf{u}_{Am}$) affect bird movements (Blomqvist and Peterz 1984), alter attendance at colonies (Birkhead 1978), and may interact with the aerodynamic performance of a species to modify rate of prey supply to chicks (Uttley et al. 1989). Oceanic currents ($\nabla_h \cdot \mathbf{u}_{Oc}$) affect bird movements directly in the case of swimming birds (Brown 1985), or indirectly by concentrating prey. The effects of atmospheric motions and ocean circulation on movements and contact rates between seabirds, fishing vessels, and nekton are largely unknown.

DIMENSIONLESS RATIOS

The relative importance of competing processes listed in equations 1-3 (Table 1)

can be evaluated through the construction of dimensionless ratios. We might, for example, take the ratio of recruitment ($\hat{R}_B$) to death rates ($\hat{D}_B$) to evaluate the relative importance of these processes in a given situation (Ford et al. 1982). Several dimensionless ratios have been used to evaluate the impact of seabirds on prey stocks. These ratios, named for convenience after the authors who used or devised them, are the Schaefer, Wiens, and Bourne ratios (Duffy and Schneider *in press*). Schaefer (1970) compared the catch rate by birds to the catch rate by fishing vessels. The resulting ratio ($Sf' = D_{N \rightarrow B} / D_{N \rightarrow V}$) scales one source of mortality to another. Literature values of Sf' range from 0.003 (Furness and Barrett 1985), to 87 (Harrison and Seki 1987). The spatial overlap and the spatial scale of catches by birds and fish vessels are rarely known; this may be one source of variation in literature values.

The Wiens ratio (Wiens and Scott 1975) Wi' is $D_{N \rightarrow B} / P_N$ where P_N is production of fish during time period of consumption $D_{N \rightarrow B}$. The Wiens ratio based on mass (rather than numbers) ranges from 0.04 (Bourne 1983) to 0.37 (Springer and Roseneau 1985).

Bourne (1983) argued that advective resupply was substantial relative to prey consumption near the Shetland Islands, but provided no quantitative estimates of either rate. The concept can be quantified as a Bourne ratio (Br'), here defined as the instantaneous loss of nekton to birds, relative to resupply by currents ($\hat{D}_{N \rightarrow B} / \nabla_h \cdot u_{oc}$). This ratio scales a demographic rate to a kinematic rate. At South Georgia Island krill consumption by the seabird colony has been estimated at 80% of the standing stock per month (Croxall and Prince 1987), or 2.7% day⁻¹. Advective resupply comes to 16% day⁻¹, using a typical current speed of 3 m s⁻¹, and a foraging radius of 80 km. The resulting ratio is 2.7/16 = 0.17, which indicates that resupply exceeds consumption of krill around South Georgia. In Hudson Bay, advective resupply within a foraging radius of 160 km comes to 1.9% day⁻¹, based on an average current speed of 0.07 m s⁻¹ (Cairns and Schneider 1990). Assuming a catch of 30% of stock over a 90 day breeding season, the Bourne ratio would be 0.16, indicating that advective resupply exceeds consumption rate.

Dimensional analysis

A complete set of ratios can be obtained by dimensional analysis (Bridgman 1922). The method is simple. One sets up a two-way table with all variables of interest listed along one side (rows) and all fundamental dimensions along the other side (columns). One then writes the appropriate exponent in each cell (e.g., +2 in the length column for a variable that is an area). This generates the dimensional matrix. The object is to form dimensionless ratios, i.e. combinations of variables, that reduce all cells in the matrix to zero. This can be accomplished by linear algebra (Langhaar 1980), or equivalently by the successive elimination method of Taylor (1974). The latter is readily grasped from an example (Appendix 2).

The results of a dimensional analysis depend on the initial choice of quantities. If we choose number of recruits R , number of deaths D , velocity of individuals relative to the fluid u_i , velocity of the fluid relative to the earth u_F , change in area occupied $\dot{A}$, and rate of demographic change $\dot{Q}$, then dimensional analysis results in three dimensionless ratios (Appendix 2). The three ratios are M' the ratio of demographic rates to divergence (movement), R' the ratio of locomotory to fluid (passive) motions, and D' the ratio of instantaneous recruitment and death rates. Diffusive (random) movements are often an

important component of fluid motions ($\nabla_h \cdot u_{Am} + \nabla_h \cdot u_{Oc}$). If a diffusive term had been included in the list of variables, then a fourth dimensionless ratio would result, the ratio of diffusive to directed motions A' .

As an example of the formal use of these ratios, M' (demography relative to kinematics) can be used to diagnose whether demographic factors (recruitment and death) or kinematic factors (e.g., shifts or contraction in range) should be further investigated as responsible for an observed decline in density ($[\dot{Q}_B] < 0$). For marine birds, values for the numerator ($\dot{Q} = \dot{R}_B - \dot{D}_B$) can be obtained from colony studies of mortality and recruitment rates. Literature values vary, but do not appear to depend on spatial scale. Kinematic values ($\dot{A}$) for birds can be obtained from flight speeds, if the spatial scale of analysis is small (flight speed $\times$ time). Flight speeds decrease with increase in scale, because birds do not fly continuously, nor in straight lines over periods of days (Jouventin and Weimerskirch 1990). Consequently, short-term flight speeds cannot be used to calculate kinematic values at larger scales. Kinematics at seasonal time scales can be calculated from speeds realized between points along the migratory route (Moissan and Sherrer 1973).

For the nektonic prey of marine birds, demographic rates ($\dot{Q}$) can be obtained from direct measurements in well-studied species, or from allometric equations relating mortality or recruitment rates to body size (Peters 1983). Kinematic rates over short distances can be calculated from allometric equations relating swimming speed to body size. For the same reasons as with birds, kinematic values of nekton at larger scales cannot be calculated from short-term swimming speeds. Turning frequency and duration of halts will determine how average speed decreases with increasing spatial and temporal scale.

The ratio of recruitment to mortality rates D' can be used to diagnose the long-term effect of an environmental perturbation on a population. Ford et al. (1982) calculated the recovery time of seabird populations around the Pribiloff Islands at several levels of oil-induced mortality, using the best available demographic and distributional data. Considerable care is needed in calculating recruitment rates, because mortality rates in seabirds decline rapidly with age between time of fledging and time of first reproduction (Jouventin and Weimerskirch 1988). Consequently, recruitment measured as number of individuals fledged will differ considerably from recruitment measured as number of offspring that reach breeding status. In a population that is maintaining itself, D' is expected to be close to unity if R_B is taken as recruitment to the breeding population. However, if R_B is taken as fledging rate, then D' is expected to exceed unity by a factor roughly proportional to the number of years of active breeding. This is because fledging rate exceeds recruitment to the breeding population. Deviations from these expectations indicate that a population is not maintaining itself.

We can also ask whether empirical ratios or ratios derived from dimensional analysis provide new insights into seabird-fisheries interactions. To do this we examined a relatively well studied situation: fishermen, pelicans, and anchovies in the California Current system (Anderson et al. 1980, Anderson and Gress 1984). Beginning with 3 empirical ratios, we found that for the brown pelican (*Pelecanus occidentalis*) all three ratios take on very small values because consumption by pelicans is small relative to anchovy catch by vessels, to anchovy production, or to anchovy drift past colonies (Anderson et al. 1980). The implicit scale of these comparisons is fairly large because

of the mobility of anchovies. Consequently, the effect of a single predator on a dominant species is negligible.

D' the ratio of recruitment to death, did reflect major changes in pelicans, anchovies, and fishermen. The pre-1970 decline and post-1970 recovery of pelicans coincided with a change in D' from less than unity prior to 1970 to greater than unity afterward (Anderson et al. 1975). For anchovies the D' ratio went through 3 phases: $D' = 1$ through the late 1960's and early 1970's, $D' > 1$ during the mid-1970's, D' slightly < 1 since, reflecting major changes in stock size at this time scale. The ratio D' for fishing vessels has been generally low in the U. S., but during the 1980's in Mexico the ratio became much greater than unity resulting in a build-up of a fleet at Ensenada; this resulted in a brief but intense anchovy fishery (Walls 1992) that collapsed in 1990. Thus, the ratio D' reflected the dynamics of change in numbers of pelicans, anchovies, and vessels at fairly large (>100 km) spatial scales.

The ratio of active to passive motions R' is large in vessels, pelicans, and anchovies, except under unusual conditions such as storms. This ratio offered little insight into interactions of pelicans, anchovys, and fishermen in the California Current system.

The ratio of demographics to kinematics M' is highly seasonal in pelicans; at the spatial scale of the foraging radius around colonies the ratio switches from much greater than unity in the breeding season, when populations are tied to colonies (Anderson et al. 1982), to much less than unity outside the breeding season, when birds move away from colonies. Similar seasonal changes occur in anchovies, which become concentrated in the southern California Bight by spawning and feeding constraints. This suggests that seasonal drops in M' of pelicans may be tied to seasonal drops in M' of anchovies. For vessels, the ratio of demographic to kinematic rates tends to be much less than unity except during the opening of a new fishery (large recruitment of vessels), or during the collapse of a fishery (large loss of vessels from the fishery). The ratio of kinematics of vessels to kinematics of fish also appears to be important, because vessels are constrained by the location of home ports, and function more efficiently when the movements of anchovies are restricted. Thus kinematic ratios of prey and predator, and the underlying energetics, may be at least as important as the ratio of demographics to kinematics within a prey or predator. Our conclusion, from examining the case of the brown pelican in south California, was that ratios of the kinematics of prey and predator cannot be ignored in understanding the dynamics of seabird fisheries interactions. A framework based on ratios within populations allowed interpretation of trends in population sizes of pelicans, anchovies, and vessels, but was too restrictive for providing insight into seabird-fishery interactions. It would be useful to undertake a similar evaluation for another system, such as alcid feeding on plankton, where passive fluid motions become important.

DISCUSSION

Comparison of ratios derived from dimensional analysis of a problem can provide information on the relative importance of competing processes. Comparison of several ratios is particularly important in cases where there are a number of competing processes,

and a single ratio does not provide full information on all processes. The ratio of recruitment to mortality D' needs to be evaluated, for example, in view of the importance of the ratio of demographic to kinematic rates (M'). If kinematic rates predominate ($M' \ll 1$), then the ratio of recruitment to mortality (D') will be less important (and less readily interpreted) than if demographic rates predominate ($M' \gg 1$).

The use of ratios is no substitute for determining the mechanism responsible for an observed decrease in a seabird population (Duffy et al. 1987). However, ratios can serve as a guide to research needed to identify causes. Ratios also indicate the relative importance of competing processes. The value of the method lies in permitting a comprehensive, rather than piecemeal, evaluation of complex ecological problems. The absence of dimensional analysis from quantitative ecology does not reflect inapplicability of the method.

The goal of research is to make reliable calculations to support decisions on conservation of marine birds. Based on our review of the literature within a comprehensive quantitative framework, several research needs have been identified. One need is for a better understanding of how processes (recruitment, death, active and passive divergence) depend on spatial and temporal scale. A second need is to identify functional relationships between terms (e.g., relation of avian recruitment ($\hat{R}_B$) to change in nekton density ($[\dot{Q}_N]$). A third need is to develop formal models of key functional relationships, with explicit treatment of spatial and temporal scales. The philosophical basis for this approach is that direct measurement is expensive and logistically impossible in many cases; the only alternative is reliable calculations from related parameters, within a consistent theoretical framework.

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APPENDIX 1. Definition and relationship of variables.

Q	Quantity of vessels Q_v , birds Q_b , or nekton Q_n . Dimensions are either count or mass.
A	Area occupied by Q_v , Q_b , or Q_n . Dimensions are length ²
$[Q]$	Density of vessels $[Q_v]$, birds $[Q_b]$, or nekton $[Q_n]$. Dimensions are length ⁻² or mass·length ⁻² .
$[\dot{Q}]$	Instantaneous time rate of change of $[Q]$. $[\dot{Q}] = [Q]^{-1} d[Q]/dt$, where t = time. Dimensions are % time ⁻¹ .
$\dot{A}$	Instantaneous time rate of change in area occupied. Dimensions are % time ⁻¹ .
u	velocity of Q in directions x and y , with respect to fixed Cartesian grid on the surface of the earth. $u = (\delta x/\delta t \ \delta y/\delta t)$. Dimensions are length time ⁻¹ .
u_{Am}	velocity of atmosphere in direction x and y , with respect to fixed grid on the surface of the earth.
u_{Oc}	velocity of ocean in direction x and y , with respect to fixed grid on the surface of the earth.
u	velocity of vessels u_v , birds u_b , or nekton u_n with respect to surrounding fluid (atmosphere or ocean). Dimensions are length time ⁻¹ .
R	instantaneous rate of recruitment of vessels (R_v), birds (R_b), or nekton (R_n). Dimensions are % time ⁻¹ .
D	instantaneous rate of loss of vessels (D_v), birds (D_b), or nekton (D_n) ($D_n = Z$ of Ricker [1975]). Dimensions are % time ⁻¹ .
$D_{N \rightarrow V}$	instantaneous loss rate of nekton (fish) to vessels. F of Ricker (1975). Dimensions are % time ⁻¹ .
$D_{N \rightarrow B}$	instantaneous loss rate of nekton (fish) to birds. Dimensions are % time ⁻¹ .
$\nabla_h \cdot u$	horizontal divergence of units of quantity Q moving at velocity u .
$\nabla_h \cdot u = (\delta u/\delta x \ \delta v/\delta y)$	Dimensions are % time ⁻¹ .
$Sf^I = D_{N \rightarrow B}/D_{N \rightarrow V}$	Shaeffer ratio, the instantaneous loss to birds, relative to instantaneous loss to fishery. Estimated as food demands of birds, divided by vessel catch (Schaefer 1970).
$W_t^I = D_{N \rightarrow B}/P_N$	Wiens ratio, where P_N is production of fish during time period of consumption $D_{N \rightarrow B}$ (Wiens and Scott 1975).
$Bt^I = D_{N \rightarrow B}/\nabla_h \cdot u_{Oc}$	Bourne ratio, the instantaneous loss of nekton to birds, relative to resupply by currents (Bourne 1983).

APPENDIX 2. Dimensional analysis.

The quantities of interest are: number of deaths (D), number of recruits (R), velocity of individuals relative to the fluid (u_i), velocity of the fluid relative to the earth (u_F), change in area occupied ($\dot{A}$), and rate of demographic change ($\dot{Q}$). The primary quantities are: length (L), time (T), numbers of individuals ($\#$). The dimensional matrix is:

	D	R	u_i	u_F	$\dot{A}$	$\dot{Q}$
L	0	0	1	1	0	0
T	0	0	-1	-1	-1	-1
$\#$	1	1	0	0	0	0

Dividing through by column 1 (D), the revised matrix becomes:

	R/D	u_i/R	u_F/R	$\dot{A}/R$	$\dot{Q}/R$
L	0	1	1	0	0
T	0	-1	-1	-1	-1
$\#$	0	-1	-1	-1	-1

Dividing through by row 2 (u_i/R), the revised matrix becomes:

	R/D	u_i/u_F	$\dot{A}/u_F$	$\dot{Q}/u_F$
L	0	0	-1	-1
T	0	0	0	0
$\#$	0	0	0	0

Dividing through by row 3 ($\dot{A}/u_F$), the final matrix becomes:

	R/D	u_i/u_F	$\dot{Q}/\dot{A}$
L	0	0	0
T	0	0	0
$\#$	0	0	0

Dimensional analysis results in the following ratios¹:

$M' = \dot{Q}/\dot{A}$, Ratio of demographic rates to divergences (movements);

$R' = \nabla_h \cdot u_i / (\nabla_h \cdot u_{Am} + \nabla_h \cdot u_{Oc})$, Ratio of locomotory to fluid (passive) motions;

$D' = R/D$, Ratio of recruits to deaths.

An additional ratio results if diffusive motions are included:

$A' =$ ratio of diffusive and inertial motions.

¹The idea of scaling active to passive motions occurred while watching a 2-year old child in a typical Newfoundland windstorm (winds 100 km hr⁻¹). The ratio was less than unity, and increased to greater than unity as the child grew older (larger). The choice of symbols is based on first initials of 4 children: Maggie Schneider, Reed Schneider, Dominique Duffy, and Alexander Duffy.

Subtidal Response of Scotian Shelf Circulation to Local and Remote Forcing. Part I: Observations

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ABSTRACT

Data collected during the Canadian Atlantic Storms Program (CASP) suggest that two primary current regimes exist on the Scotian Shelf during winter. Moorings inside the 100-m isobath feature currents that are parallel to the general bathymetry and have small eastward mean velocities. The time-varying part of the flow is nearly rectilinear alongshelf at typical maximum velocities of $0.2\text{--}0.3\text{ m s}^{-1}$ and oscillates on 2–5-day periods in response to meteorological forcing. The current at locations beyond the 100-m isobath exhibits a persistent westward flow of about 0.3 m s^{-1} , denoting the dominance of the Nova Scotian Current, although smaller magnitude along- and cross-shelf fluctuations occur at synoptic frequencies. Flow in both regions is largely uniform with depth at this time of year.

The velocity response to local and remote sources of forcing was examined using a frequency (ω)-dependent multiple regression model. Flow is dominated by nonlocal forcing at $\omega < 0.2$ cpd; alongshelf wind stress is the principal local influence at low frequencies. Remote forcing is less important at higher frequencies, while the role of local cross-shelf wind stress is greater. The effect of local wind forcing is generally small and varies substantially on horizontal scales of order 10 km. Current typically lags wind stress by about $30^\circ\text{--}45^\circ$ at $\omega < 0.5$ cpd; the response to alongshelf wind stress also suggests a phase propagation to the west. The typical response to alongshelf wind forcing is consistent with previous quasi-steady observations and model results from the Scotian Shelf. The contribution of cross-shelf wind stress is limited to a near-surface flux in the synoptic band. The remote response decreases offshore and to the west and propagates westward, in the direction that coastally trapped waves propagate. The current response to local and remote forcing is uniform with depth at nearly all locations. Local and remote contributions to alongshelf velocity, integrated across the mooring array, are in geostrophic balance with the cross-shelf subsurface pressure (SSP) gradient. Together, the two wind stress components and a SSP record representing nonlocal forcing explain 40%–80% of alongshelf flow, compared to 95% of the SSP signal.

Some of the large-scale flow features are consistent with variations seen in SSP data. The most obvious similarity is the remotely forced response. However, these results also reveal substantial variations in the current on scales of 10–100 km that are not reflected in the SSP field. Irregular shelf bathymetry is thought to induce the observed variations in circulation. This study also demonstrates the need to include remote forcing effects, in the form of a properly prescribed backward boundary condition, in shelf circulation models.

1. Introduction

The Scotian Shelf region off eastern Canada lies in the path of numerous winter cyclones, due to its location relative to continental land masses and the distribution of upper-atmospheric circulation patterns. The track, direction, and intensity of these storms are variable. In general, the storms are quite severe, featuring extremely low central pressures, high winds, and intense precipitation (cf. Lewis and Moran 1984). Like most midlatitude continental shelves, meteorological forcing is an important source of energy to Scotian Shelf dynamics at 2–10-day periods (Petrie and Smith 1977; Smith et al. 1978; Sandstrom 1980; Schwing

1989). The Canadian Atlantic Storms Program (CASP), formulated to study the nature of East Coast winter storms (Stewart et al. 1987) and coordinated with the Genesis of Atlantic Lows Experiment (GALE) along the eastern United States, included an intensive oceanographic field sampling program to examine how winter storms drive circulation on the inner Scotian Shelf (Anderson et al. 1989; Anderson and Smith 1989).

Previous analysis of the subinertial, meteorologically driven response of subsurface pressure (SSP) during CASP has provided considerable insight to the Scotian Shelf dynamics (Schwing 1989). Schwing found that subinertial variations in SSP are highly coherent throughout the Scotian Shelf region, and well correlated to fluctuations in wind stress forcing over the shelf. A multiple regression model showed that alongshelf stress is the primary source of local meteorological forcing, although nonlocally generated motions, as approxi-

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mated by Louisbourg SSP at the eastern end of the province (Fig. 1), are also important. Wind stress and nonlocal forcing combine to explain over 90% of SSP variance at subinertial frequencies.

Schwing (1989) also concluded that the amplitude of the SSP response to local wind forcing increases from east to west. The phase of the response also propagates to the west. Time-dependent solutions to a simple, frictional numerical model that features spatially uniform alongshelf wind-stress forcing and idealized bathymetry closely resemble the observed wind-forced response, as well as the pattern found by Csanady (1978) for the steady arrested topographic wave model, and suggest that the quasi-steady limitations imposed by the long-wave and rigid-lid approximations are valid for explaining SSP variations at synoptic and lower frequencies. The amplitude and phase of the nonlocal response were found to be consistent with frictional coastally trapped wave (CTW) theory, the most direct evidence of shelf wave activity on the Scotian Shelf to date.

The SSP signals are related to transport through the equations of motion and continuity, and can be considered to be integral measures of the circulation regime (cf. Rhines 1977, pp. 196–202). Because of this, we may expect the large-scale SSP and current responses to meteorological forcing to be complementary. Thus,

the interpretation of the SSP results in Schwing (1989) can be verified by an examination of the CASP current meter records, and vice versa.

However, density stratification and mesoscale variations in bathymetry or the forcing field may induce variations in the current on small vertical and horizontal scales. Because sea level integrates depth-dependent current variability, vertical differences in velocity are “smoothed over” in SSP observations. Similarly, flow over highly irregular bathymetry, or forced by a spatially complex wind stress, will feature smaller horizontal length scales than will SSP (Willebrand et al. 1980). As Rhines (1977) observed regarding the relationship between pressure and its derivative velocity, “Integration smooths, differentiation roughens.” Therefore, SSP is likely to be more coherent with large-scale forcing than is the current. Spatial coherence scales within the current field are also probably smaller.

It also has been suggested that the barotropic modal structure of remote, or free, energy in currents is different from that in SSP (Hsieh 1982). Hsieh notes that velocity observations reflect the structure of the free response more accurately, since SSP data are strongly biased for the lowest mode, and because “the ratio of potential to horizontal kinetic energy is . . . very small for shelf waves.” Thus, while similar patterns in the response of each may verify the importance of certain

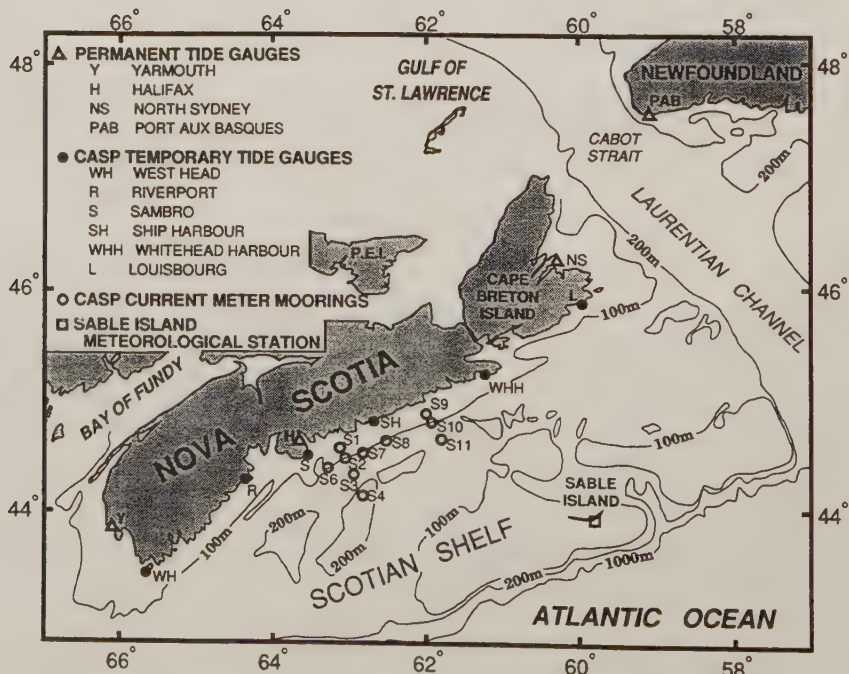


FIG. 1. Location map showing positions of CASP current meter moorings and coastal subsurface pressure stations. Wind data obtained at Sable Island AES meteorological station.

dynamical processes, it cannot be assumed that the response of the current regime will be identical to that of the SSP field. An analysis of SSP provides only a foundation of the dynamics; current observations allow mesoscale and baroclinic circulation features to be defined.

In this study, the response of the subinertial circulation on the Scotian Shelf to local and remote forcing is described and interpreted, using statistical techniques applied previously to SSP observations (Schwing 1989). Results are compared to those from the SSP analysis to confirm the conclusions of that investigation. In particular, the behavior of the current response to nonlocal forcing may verify the existence of CTWs on the Scotian Shelf, as suggested by the SSP results. The current response also provides information on mesoscale variations that are otherwise covered up by the integrated response of the pressure field. The potential importance of baroclinic motions, which cannot be discerned from SSP data, can be determined as well. The observed current response described here is compared to numerical model results in a companion paper (Schwing 1992).

In section 2, the morphology of the Scotian Shelf is briefly described, since it may contribute to variations in the velocity field. The circulation observed during CASP is described in section 3 and compared to wind stress and SSP in time series and spectral formats. A frequency-dependent regression analysis of the current response to local and remote forcing is applied in section 4, and the role of each forcing term is evaluated. Section 5 provides a discussion of these results, relating them to SSP results from Schwing (1989), to other regional studies, and to existing and potential dynamical models that may be effective in explaining circulation patterns on the Scotian Shelf.

2. Physical setting

The Scotian Shelf lies offshore from Nova Scotia in a south-southeasterly direction (Fig. 1). Its length is about 700 km, while its width, as defined by the 200-m isobath at the shelf break, varies from ~250 km at its eastern end to ~150 km to the west. The coastline is generally straight, with periodic headlands and bays having topographic scales $O(10\text{--}20\text{ km})$. Nearshore isobaths ($<100\text{-m}$ depth) follow the trend and variations of the coastline. However, much of the shelf's bathymetry is highly irregular, particularly over the eastern portion of the shelf. At distances greater than ~40 km from the coast, the typical depth of 100–150 m is interrupted by several bathymetric anomalies of glacial origin, including basins featuring depths of more than 200 m and banks that shoal to 50 m and less. These have typical horizontal length scales $O(50\text{--}100\text{ km})$. Unlike the continuous continental shelf off the eastern United States, the Scotian Shelf is bathymetrically isolated, by deep channels, from the Grand Banks

to the east and Georges Bank to the west. The eastern boundary of the shelf is defined by the Laurentian Channel, with a typical width of ~100 km and depth of ~400 m. The smaller Northeast Channel, west of the Scotian Shelf, extends into the Gulf of Maine toward the Bay of Fundy.

The abrupt changes in Scotian Shelf bathymetry and its relative isolation from regions to the east and west suggest the existence of a complex circulation for this shelf. Irregular bathymetry is likely to affect the flow in several ways. The importance of direct wind forcing over the Scotian Shelf will vary greatly, from dominant over the strongly frictional shallow regions to nearly negligible over the deep basins. Distantly forced propagating motions (i.e., CTWs) no longer have a smooth, continuous wave guide (Wilkin and Chapman 1987). Combined with the large changes in depth associated with bathymetric features on and adjacent to the shelf, it is possible that such propagations are scattered and dissipated on small spatial scales, as postulated by Wilkin and Chapman (1987) and others. If this effect is very strong near the source of such motions, then nonlocal forcing may have only a minor influence on the Scotian Shelf circulation. Alternatively, local scattering could result in enhanced small-scale variability in the circulation. Irregular bathymetry may also act to steer flow along isobaths (Wright et al. 1986), and even produce variability in the circulation in association with, and on the horizontal scales of, bathymetric features (Haidvogel and Brink 1986). These factors will be examined using a numerical model featuring realistic bathymetry (Schwing 1992), and should be kept in mind regarding the observations described below.

3. Observations

a. Methods

Current meter data described here were collected at ten moorings deployed on the Scotian Shelf from November 1985 to April 1986 as part of the CASP field experiment (Figs. 1 and 2). The moorings were arranged into two cross-shelf lines near Halifax (S1–S4) and Liscomb (S9–S11), and an alongshelf line situated on the 100-m isobath (S2, S6–S8, S10). The maximum extent of the array, approximately 65 km offshore and 120 km in the alongshelf direction, and close spacing of the moorings allowed mesoscale variations in the current field of order 10–100 km to be detected.

All velocity data were collected with Aanderaa RCM4S recording current meters, with a threshold of 1.5 cm s^{-1} and an accuracy of $\pm 1\text{ cm s}^{-1}$ and $\pm 5^\circ$ in speed and direction for a velocity range of 5–100 cm s^{-1} . A total of 28 current meters (out of 34 deployed) provided sufficiently long time series of quality data to be analyzed using the spectral techniques described below. Current velocities were rotated into

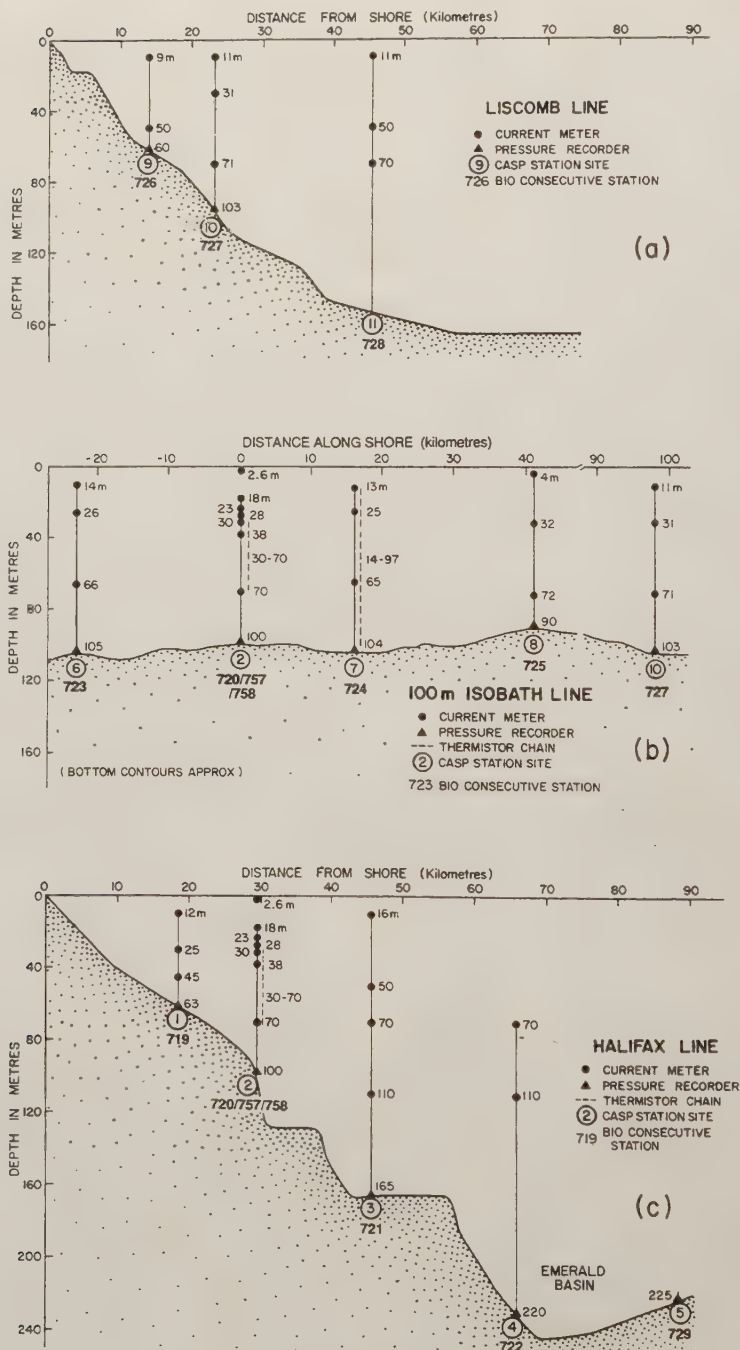


FIG. 2. Profile of (a) Liscomb current meter mooring line, (b) 100-m isobath current meter mooring line, and (c) Halifax current meter mooring line.

alongshelf ($+v = 68^\circ\text{T}$) and cross-shelf ($+u = 158^\circ\text{T}$) components, based on the typical coastline orientation. The principal axes of variation for most current time series were very similar to the alongshelf coordinate (Anderson and Smith 1989). Components were then low-pass filtered with a 129-weight Cartwright filter [0.036 cph (28 h) quarter-power cutoff] to remove tidal and inertial energy, and resampled at 6-hourly intervals. The bulk of the results refer to observations from the 100-m isobath moorings (Fig. 2b) as an indicator of alongshelf trends, and the Halifax line (Fig. 2c) for variability across the shelf.

Wind observations from the Sable Island Atmospheric Environmental Service (AES) station were chosen to represent meteorological conditions over the Scotian Shelf (Petrie and Smith 1977). Alongshelf (τ^y) and cross-shelf (τ^x) wind stress components were estimated at 1-h intervals from wind speed and direction, using the quadratic stress law with a variable drag coefficient (Smith and Banke 1975). The wind stress series were filtered and resampled in the same manner as the current series. For further information on the CASP deployment and data collection and processing, refer to Lively (1988) and Anderson and Smith (1989).

Power spectra for all series were calculated according to Carter and Ferrie (1979). The 32 frequency bands each had a bandwidth of 0.0625 cycles per day (cpd). Spectral results were averaged over $n = 14$ blocks of data with 50% overlap, giving $\nu = 22.9$ effective degrees of freedom (Garrett and Toulany 1982).

b. Time series

Low-passed current meter time series define two distinct circulation regimes on the inner portion of the Scotian Shelf (Fig. 3). Stations inside the 100-m isobath, represented by S1, typically featured a current parallel to the general bathymetry (Fig. 3a). Although the means of these records are small and typically to the east (Anderson and Smith 1989), the time-varying current was nearly rectilinear and oscillated between eastward and westward flow at periods on the order of 2–5 days. A visual comparison with Sable Island wind stress indicates a close correspondence of wind, current, and SSP events. Maximum velocities were 0.2–0.3 m s^{-1} .

The current beyond the 100-m isobath exhibited a persistent alongshelf flow to the west with average values of 0.3 m s^{-1} in the surface layer (Figs. 3c,d). These velocities suggest that the Nova Scotian Current dominates the flow outside the 100-m isobath (Drinkwater et al. 1979; Anderson and Smith 1989), although the geostrophic transports estimated by Drinkwater et al. (1979) from the baroclinic field are approximately half as large as those observed during CASP (Anderson and Smith 1989). Cross-shelf variations in flow, as well as changes in the magnitude of the alongshelf current, occurred at 2–5-day periods, again suggesting a possible

meteorological response. However, the amplitudes of such variations were much smaller than those observed in shallower water.

Moorings near the 100-m isobath, typified by S2 (Fig. 3b), experienced the net westward flow seen farther offshore, as well as alongshelf current reversals that suggest the wind-forced response of the nearshore region. Time series (Fig. 3) and progressive vector plots (Fig. 4) of near-surface instruments at S1–S3 clearly demonstrate these trends; S2 and S3 exhibit the same general pattern. However, the cumulative displacement was much greater at S3. Higher-frequency oscillations, presumably associated with the passage of atmospheric pressure systems, dominate the flow at S1, and are more evident at S2 than at S3.

A comparison of instruments on a single mooring suggests the flow is essentially uniform with depth (Fig. 3). The water column closer to shore ($h < 50$ m) is well mixed (Fig. 5), presumably by a combination of surface and bottom stress. Some reduction in velocity with depth occurred in the outer region of the array. The historical position of the February front (defined by the $\sigma_t = 25.5$ isopleth) runs through S3 and S4 at about 30–50-m depth, intercepting the bottom near the 100-m isobath (Drinkwater and Taylor 1982). Hydrographic observations at the beginning and end of the CASP field experiment indicated a similar structure (Fig. 5). Thus, some baroclinically controlled events may occur in deeper water, as suggested by the S3 time series (Fig. 3c).

However, the fact that velocities observed during CASP were substantially larger than the geostrophic currents estimated from historical density measurements by Drinkwater et al. (1979) suggests that the circulation beyond the 100-m isobath was predominantly barotropic, particularly in the upper 50–100 m (Anderson and Smith 1989). Water mass properties (temperature, salinity, and density) measured at each mooring (Lively 1988), as well as hydrographic surveys conducted at the beginning and end of the field experiment (Fig. 5), verified that baroclinic processes were minimal near the surface and throughout the inner portion of the array, but may have influenced the circulation in deeper areas of the shelf. More important, density variations at synoptic (<10 d) periods were small relative to longer-period fluctuations (Lively 1988). The density field changed relatively little over the course of the experiment (Fig. 5). Thus, the baroclinic contribution can be thought of as a relatively constant background flow added to the higher-frequency (barotropic) fluctuations of interest in this study.

A visual examination of the alongshelf current field suggests that coherence length scales are quite large in the nearshore (S1 vs S9) region of the Scotian Shelf but reduced farther offshore (S3 vs S11) (Fig. 6a). Some variation appears along the 100-m isobath (Fig. 6b). Most subinertial events were observed throughout

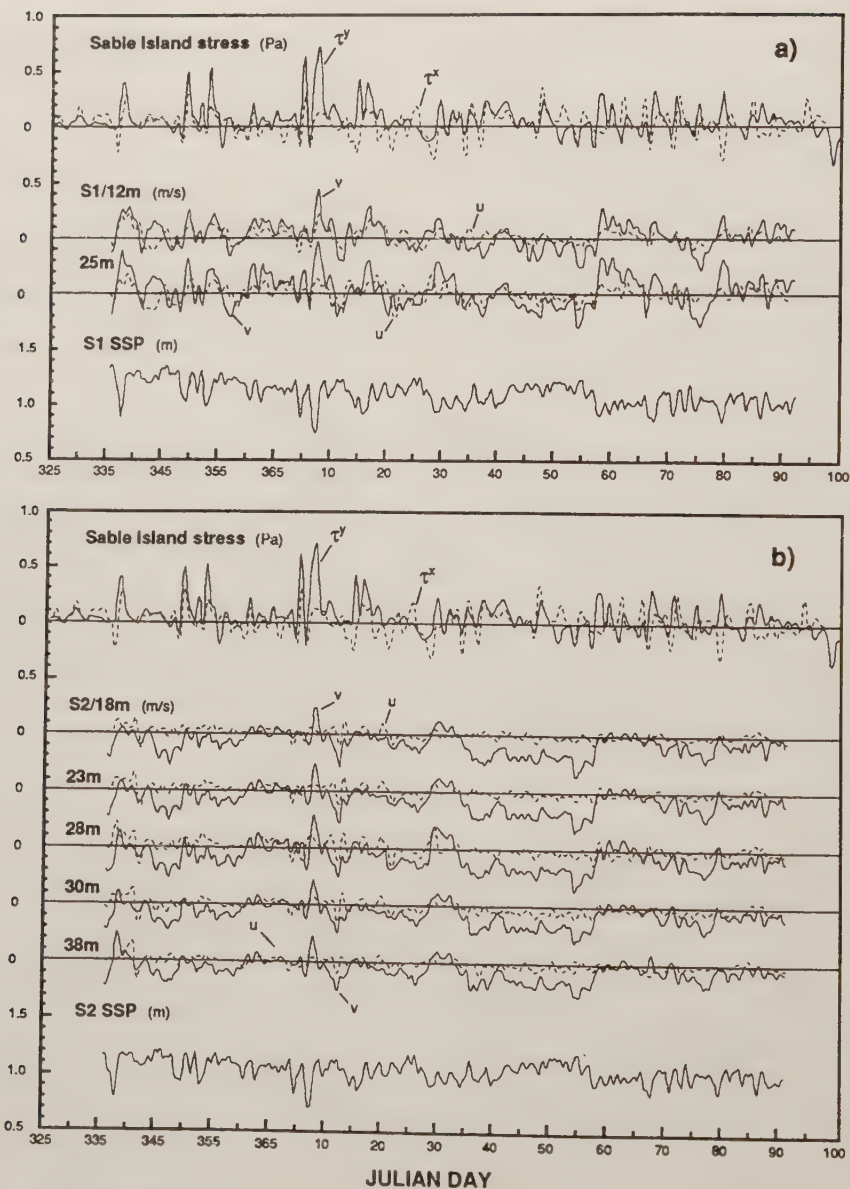


FIG. 3. Low-pass filtered time series of current meter components at (a) S1, (b) S2, (c) S3, and (d) S4. Solid line denotes alongshelf (v) component, positive to east. Broken line denotes cross-shelf (u) component, positive offshore. Low-passed bottom pressure, alongshelf (τ^y), and cross-shelf (τ^x) Sable Island wind stress

the array. However, substantial differences in the magnitude and direction of flow during individual events occurred on scales as small as 10 km. Alongshelf velocity time series are generally correlated at the significant frequencies discussed below, but no clear pattern is apparent that allows coherence length scales to be quantified.

c. Power spectra

The presentation of low-passed current power spectra in variance-preserving form reflects the relationship between wind stress, current, and bottom pressure at locations inside the 100-m isobath (Fig. 7). The variance distribution of Sable Island wind stress (Fig. 7a)

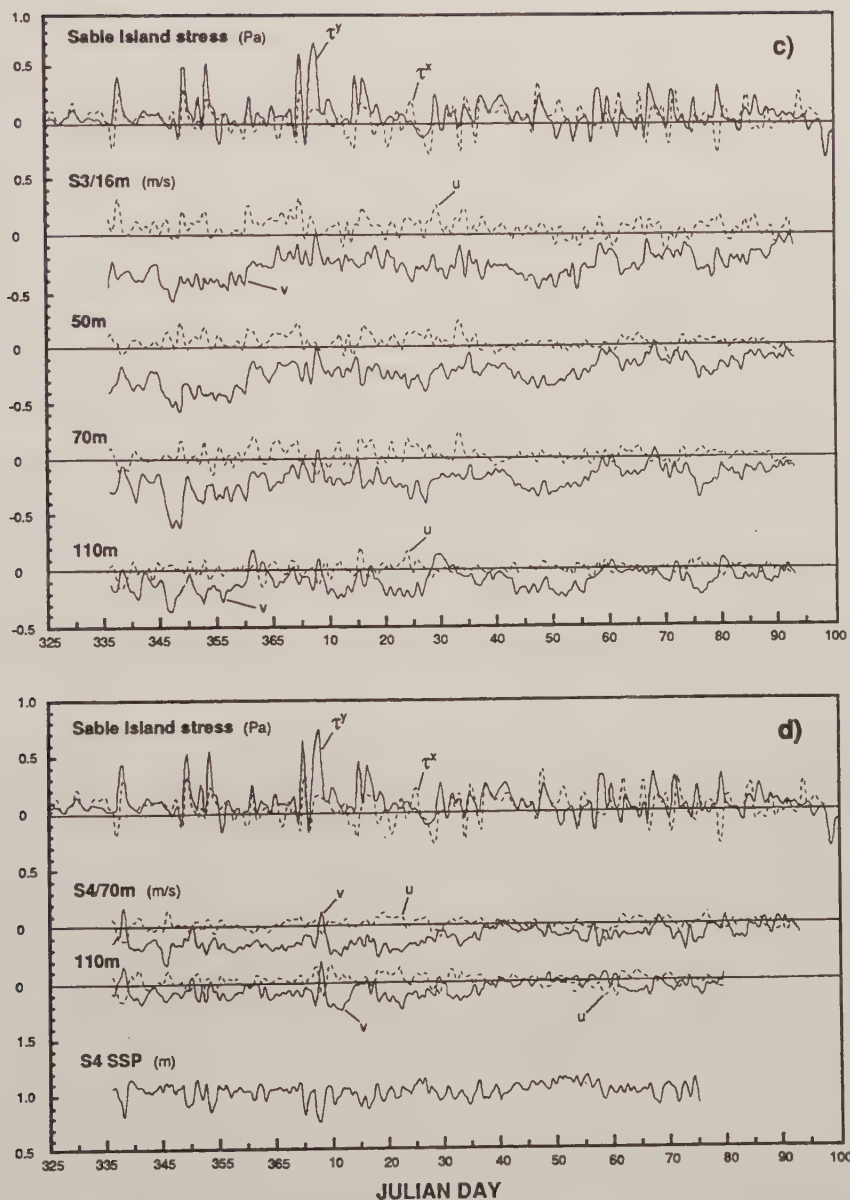


FIG. 3. (Continued) series are included for reference. Vertical axis units are pascals for wind stress, meters per second for velocity, and meters for bottom pressure.

and SSP on the Halifax line and at Sambro, a coastal site near the array (Fig. 7b), can be separated into low-frequency (≤ 0.125 cpd) and synoptic (0.2–0.5 cpd) bands containing 20%–40% and 50%–65% of the variance, respectively. Alongshelf current at S1 (Fig. 7c)

peaks in two bands, 0.125 and 0.438 cpd. The gap between these bands in the nearshore current spectra is deeper than that seen in the wind stress and SSP spectra, and the relative amount of current variance in the lowest frequency bands is greater. Cross-shelf current vari-

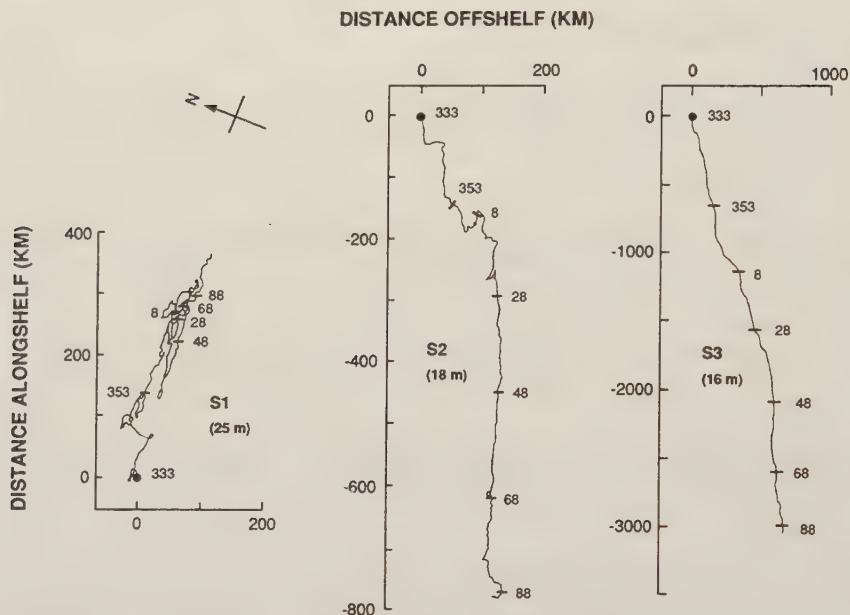


FIG. 4. Progressive vector plots comparing low-passed near-surface current records at S1 (25 m), S2 (18 m), and S3 (16 m). Tick marks denote Julian day in 1985-86. Note change in scale for S3 plot.

ance is distributed in a similar fashion, but 2-4 times less energetic at all frequencies.

At the 100-m isobath and beyond, current variance is greatly reduced at $\omega > 0.125$ cpd (Figs. 7d,e). Only at S11 (not shown) did current exhibit substantial variance at higher frequencies. Spectral variance at the lowest frequencies generally decreases seaward (cf. Figs. 7c-e) and with depth (Fig. 7d). A notable exception is S3, where variance consistently *increases* with depth at $\omega < 0.25$ cpd (Fig. 7e). With the exception of S2, where variance is noticeably reduced at all frequencies, near-surface v along the 100-m isobath displays spectra very similar to those in Fig. 7d. In general, current spectra are more "red" than those of wind stress and SSP.

Autospectral variance values in the cross-shelf component of velocity are much smaller than alongshelf variance at $\omega < 0.2$ cpd, but do not decrease as rapidly with frequency at offshore moorings. At many stations, u and v variance is nearly equal at synoptic and higher frequencies. Thus cross-shelf flow was relatively more important farther away from the coast, consistent with the magnitude of the 2-5-day oscillations in u and v noted in the time series. These results suggest that either bathymetric steering is minimal at deeper stations (i.e., bottom friction is less important, and other processes may control the circulation) or the coastline does not properly represent the local along-isobath orientation in the offshore region.

4. Statistical model

The response of SSP to meteorological forcing was estimated by Schwing (1989) using a hierarchy of multiple linear regression models in the frequency (ω) domain (Jenkins and Watts 1968; p. 493). The model that gave both the greatest statistical correlation and the most dynamically consistent results included terms that accounted for local wind stress and nonlocally forced contributions to SSP. Therefore, the response of current to meteorological forcing is described using the model

$$V(\omega) = \alpha T^y(\omega) + \beta T^x(\omega) + \gamma S^{NL}(\omega) + \epsilon(\omega). \quad (1)$$

The variables V , T^y , T^x , and S^{NL} in (1) define Fourier transforms of v , τ^y , τ^x , and SSP^{NL} , respectively, where SSP^{NL} , approximated by SSP at Louisbourg on the eastern edge of the province (Fig. 1), is a representation of the nonlocally forced contribution to SSP. The coefficients α , β , and γ are complex transfer functions and ϵ is the residual error associated with each model. Least-squares estimates of α , β , and γ give the amplitude ($|\alpha|$, $|\beta|$, $|\gamma|$) and phase (ϕ_α , ϕ_β , ϕ_γ) of the SSP response to each individual forcing term as well as the multiple coherence squared (R^2) due to the model for each frequency band centered at ω .

The determination of the least-squares estimates of the response functions uses the partial cross spectrum, which takes into account the cross-spectral relationship

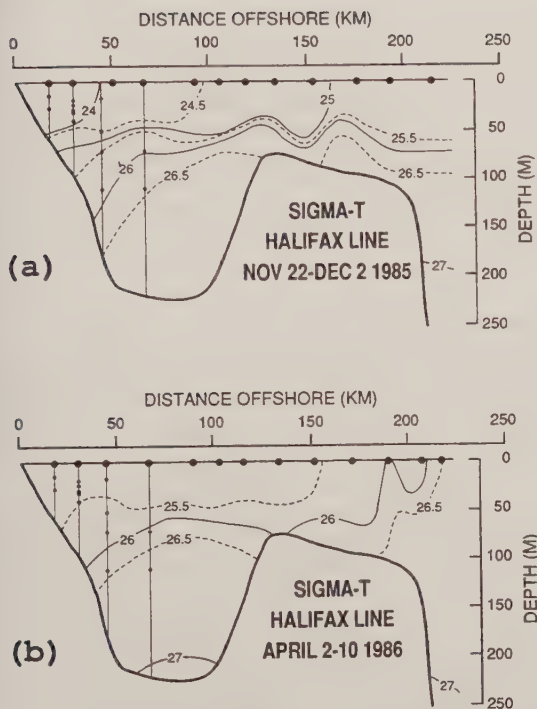


FIG. 5. Vertical density structure for a cross-shelf line extending through the Halifax current meter mooring line for (a) 22 Nov–2 Dec 1985 and (b) 2–10 Apr 1986. Current meter positions denoted by small circles on vertical lines. Larger circles denote location of hydrographic stations. Adapted from Lively (1988).

between the three independent variables (Jenkins and Watts 1968; pp. 485–487). For example, the response of current to nonlocal forcing is based on the dependence of v on SSP^{NL} after the effects of local wind stress (τ^y and τ^x) on the flow have been considered. This eliminates concern that the response of the dependent variable to any independent variable may be biased because the forcing terms are highly coherent. Garrett and Toulany (1982) provide further details of this technique.

Further analysis of the velocity response will focus on the alongshelf current component because it contains a majority of the low-frequency variance, and because results of the cross-shelf current analysis are statistically insignificant in most cases. Figures 8–10 summarize the response of v to SSP^{NL} , τ^y , and τ^x , the three forcing terms in the statistical model (1), at 0.125, 0.438, and 0.625 cpd. These complicated figures require a thorough orientation before the statistical results are described. Each figure presents a series of Argand, or phasor, diagrams for stations along the Halifax line [part (a) of each figure] and along the 100-m isobath [part (b)]. Each vector represents the amplitude and phase of the current response (referenced to the en-

closed compass rose) to the three forcing terms at each current meter. The origin of each set of vectors is referenced to the distance scale at the top of each figure.

Bold vectors, with instrument depth shown near the arrow in large type, denote transfer functions whose amplitudes are significantly different from zero at the 0.05 level; lighter vectors with smaller-type depths are not significant. Amplitude is expressed in $m s^{-1}/Pa$ for τ^y and τ^x , and $m s^{-1}/m$ for SSP^{NL} forcing. Positive phase denotes current leads forcing. Vectors that rotate in a clockwise manner along a certain direction imply a phase propagation in that direction.

For example, consider the response at S1 to SSP^{NL} at 0.125 cpd (top row, left in Fig. 8a). The SSP variations (denoted by P) lag SSP^{NL} by 13° , and change 0.66 m for every 1-m change in SSP^{NL} . The alongshelf velocity at 25 m lags SSP^{NL} by 180° (i.e., flow is maximum to the west when SSP^{NL} is at its maximum) and changes by about $1.6 m s^{-1}$ for every 1-m change in SSP^{NL} . The gain of v at 12 m to nonlocal forcing is $1.4 m s^{-1}/m$; v at 12 m lags the current at 25 m by 18° .

Figure 11 presents a series of histograms representing the alongshelf velocity variance preserved at each instrument, whose depth is given below the bar. Each is divided into four regions that represent the percentage of variance accounted for by each independent variable and a residual. The magnitude of each portion is the product of the current variance, total coherence squared (R^2), and the partial coherence between current and that forcing term, divided by the sum of the partial coherences. The R^2 value is given above the bar; all are significant to the 99% level. The responses of SSP at each mooring due to SSP^{NL} , τ^y , and τ^x (denoted by P), discussed in detail in Schwing (1989), are included in Figs. 8–11 for reference.

The selection of Louisbourg SSP as a representation of nonlocal forcing is somewhat arbitrary. It is based on the concept suggested by Gill and Schumann (1974), and others, that shelf motions at any point can be linearly separated into local (v^L) and nonlocal (v^{NL}) contributions:

$$v(x, y, t) = v^L(x, y, t) + v^{NL}(x, y, t).$$

For the Scotian Shelf, the term v^L defines the locally forced influence; that is, the velocity response to wind stress over the Scotian Shelf. That portion of v whose source lies beyond the Scotian Shelf is defined by v^{NL} , and represented by Louisbourg SSP . Results consistent with the dynamical model of Schwing (1989) indicate that the response of Louisbourg SSP to Sable Island wind stress is small at synoptic and lower frequencies, suggesting that the SSP signal there contains a significant amount of energy originating from a distant source. The anomalous autospectrum at Louisbourg (Fig. 7b) indicates this is true at higher frequencies as well. Finally, its location adjacent to the Cabot Strait makes Louisbourg SSP a good diagnostic of energy

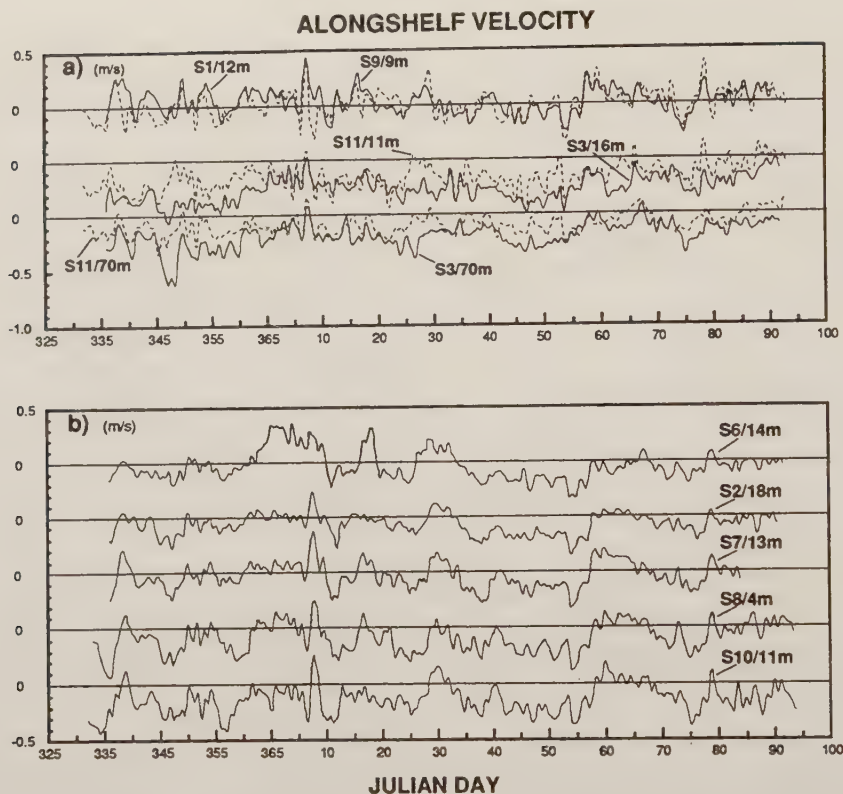


FIG. 6. Low-pass filtered time series comparing alongshelf current components at various stations in the array. (a) Comparison between S1 (12 m) (solid line) and S9 (9 m) (broken line), and between S3 (16 and 70 m) (solid lines) and S11 (11 and 70 m) (broken lines). Vertical axis units are meters per second. (b) Comparison of alongshelf current components along 100-m isobath at S6 (14 m), S2 (18 m), S7 (13 m), S8 (4 m), and S10 (11 m).

crossing the Laurentian Channel or propagating out of the Gulf of St. Lawrence. The separation of velocity into local and remote contributions will be applied further in the accompanying modeling study (Schwing 1992).

a. $\omega = 0.125$ cpd

Except for the deepest mooring S4, the alongshelf velocity field at $\omega < 0.2$ cpd, represented by the results at 0.125 cpd, is dominated by nonlocal forcing, both in terms of the response amplitude $|\gamma|$ (Fig. 8) and the percentage of variance attributed to SSP^{NL} (Fig. 11). Values of $|\gamma|$ are typically 1.0 – 1.5 $m\ s^{-1}/m$ and decrease to the west by $\sim 25\%$ over an alongshelf distance of ~ 120 km (Fig. 8b). The cross-shelf decrease in $|\gamma|$ is much larger, about 25% between S1 and S3 (~ 30 km), and a factor of nearly 5 at the deepest mooring (Fig. 8a).

The phase ϕ_γ is about 180° in the nearshore region, implying that a maximum velocity to the east (west)

occurs when Louisbourg SSP is at a minimum (maximum). Assuming small fluctuations in sea level at the shelf break, the nearshore alongshelf velocity is qualitatively consistent with a geostrophic balance by η_{xx} , the cross-shelf pressure gradient. The response of SSP also implies this. The results also suggest an offshore phase propagation in the Halifax line, such that v at S3 is nearly in quadrature with SSP^{NL} . Here an eastward (westward) flow coincides with a rising (falling) SSP signal. Thus, it appears that friction dominates at shallow stations, but weakens offshore.

With the exception of S8, remotely forced currents display a consistent decrease in phase to the west, in the direction that free CTWs propagate (Fig. 8b). The phase speed over this distance is estimated to be 2 – 4 $m\ s^{-1}$, comparable to a second-mode CTW phase speed of 2.5 $m\ s^{-1}$ calculated for the Scotian Shelf from the coastal SSP data (Schwing 1989). However, the mooring array size was small relative to the free wavelength, and confidence limits are sufficiently large such

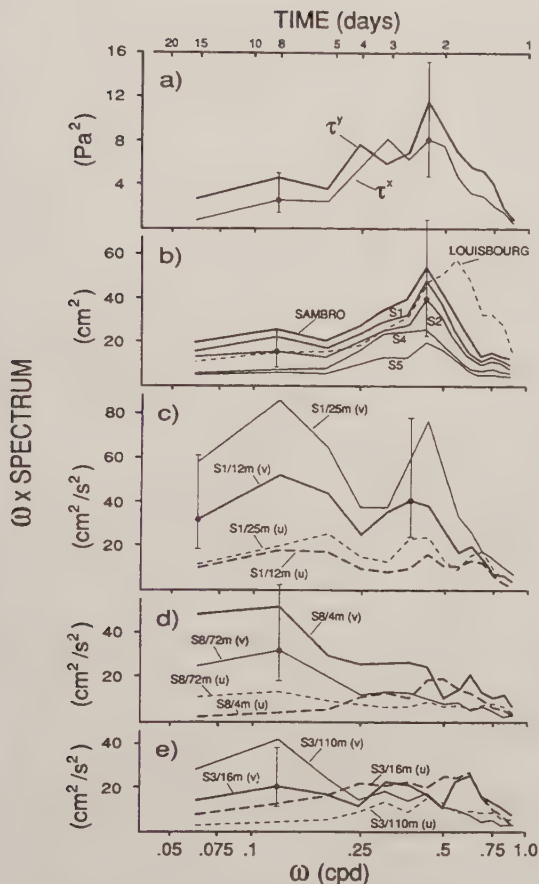


FIG. 7. Power spectra (variance preserved) of low-pass filtered time series for (a) Sable Island alongshelf (τ^y) and cross-shelf (τ^x) wind stress, (b) bottom pressure (SSP) from Halifax line (S1–S4) and coastal stations at Sambro and Louisbourg, and current components at (c) S1, (d) S8, and (e) S3. Representative 95% confidence intervals are shown.

that phase is not statistically different between stations. An array with a greater alongshelf extent is required to resolve with confidence the phase speed of the current response to nonlocal as well as local forcing.

The gains of v to local wind stress forcing ($|\alpha|$ and $|\beta|$) at 0.125 cpd are typically 0.25–0.50 $\text{m s}^{-1}/\text{Pa}$, but most are not significantly different from zero due to low coherence between wind stress and current. At most locations v lags τ^y by about 45° and τ^x by 120° – 140° (where $|\beta|$ is significant), consistent with the cyclonic rotation of wind stress during the passage of an atmospheric low to the south of the array. The most significant features in the local wind-forced response are the generally small gains and the lack of any consistent pattern from station to station. Note particularly the anomalously small response at S2, consistent with

the reduced variance observed there, as well as the relatively large response to τ^y at S7 and τ^x at S6, the westernmost mooring. These results all suggest that mesoscale variability on horizontal scales of 10–100 km is substantial in the current field, despite the absence of such variability in the SSP signal.

The velocity response to local and nonlocal forcing is uniform with depth at all stations except S3 and S7. The phase of velocity relative to SSP^{NL} and τ^x at 110 m at S3 leads the current above it by $\sim 50^\circ$, consistent with theoretical estimates of the vertical phase shift associated with baroclinic instability (P. C. Smith, personal communication).

Finally, consider the percentage of current variance due to each independent variable, as shown in the histograms in Fig. 11. Nonlocal forcing contributes 50%–80% of the explained variance; τ^y generally accounts for much more variance than τ^x , and tends to be more important where the role of SSP^{NL} is diminished. However, the percentage due to τ^x is similar to or greater than that for τ^y in some cases (e.g., S8, S10). Thus, unlike the marginal SSP response to τ^x , the effect of cross-shelf wind stress on the current cannot be ignored. Total variance squared at 0.125 cpd varied between 0.5 and 0.8, smaller than the typical $R^2 = 0.95$ for SSP data.

The actual velocity amplitude contributed by each forcing term can be compared by estimating the amplitude of SSP^{NL} , τ^y , and τ^x from the spectral variance of each, then multiplying by the associated gain. For typical values of $|\alpha|$, $|\beta|$, and $|\gamma|$, the amplitude of the alongshelf current forced by τ^y is 1–2.5 cm s^{-1} , slightly less for τ^x , and 3–5 cm s^{-1} due to SSP^{NL} . Thus, local wind stress forcing is of secondary importance to the nonlocal contribution at low frequencies. Although $|\beta|$ values are similar to $|\alpha|$, recall that τ^y variance is 2–3 times greater in most frequency bands (Fig. 7a). Thus, the actual role of alongshelf wind stress forcing is greater. In addition, τ^y is typically more strongly correlated with v , so confidence intervals are generally larger for $|\beta|$ than $|\alpha|$.

b. $\omega = 0.438$ cpd

The most striking change in the current response at higher frequencies ($\omega > 0.2$ cpd) is the greatly reduced response to SSP^{NL} . Values of $|\gamma|$ at 0.438 cpd are 0.25–0.50 $\text{m s}^{-1}/\text{Pa}$, and generally decreases offshore (Fig. 9a) and to the west (Fig. 9b). As noted at 0.125 cpd, ϕ_γ is about 180° . A geostrophic balance with the remote SSP response is again suggested. No trend in phase speed is apparent.

The magnitudes of the τ^y responses at 0.125 and 0.438 cpd are similar on and inside the 100-m isobath. However, responses at offshore stations are weaker at 0.438 cpd (e.g., S3, S4, S7). Here v lags τ^y by about 8 h at S1, with an increased lag away from the coast (Fig. 9a); $|\alpha|$ also decreases sharply offshore. In contrast,

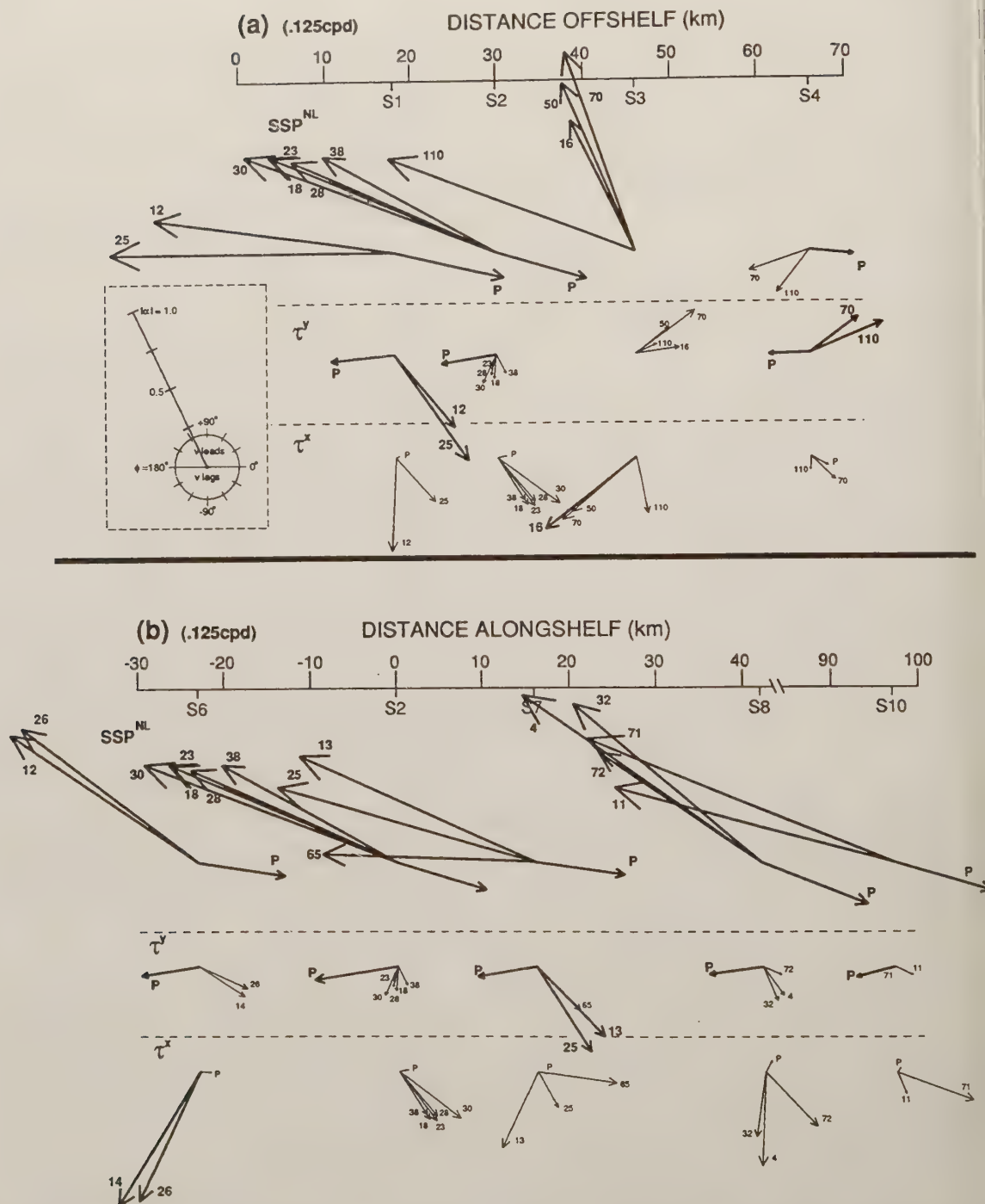


FIG. 8. Response of low-passed alongshelf current at 0.125 cpd to the forcing terms SSP^{NL} , τ^y , and τ^x in the statistical model (1) for stations in the (a) Halifax line and (b) 100-m isobath line. Vectors describe amplitude and phase of response (bold vectors and depth values denote 95% significance). SSP results from Schwing (1989), denoted by P , included for reference. Refer to text for further details.

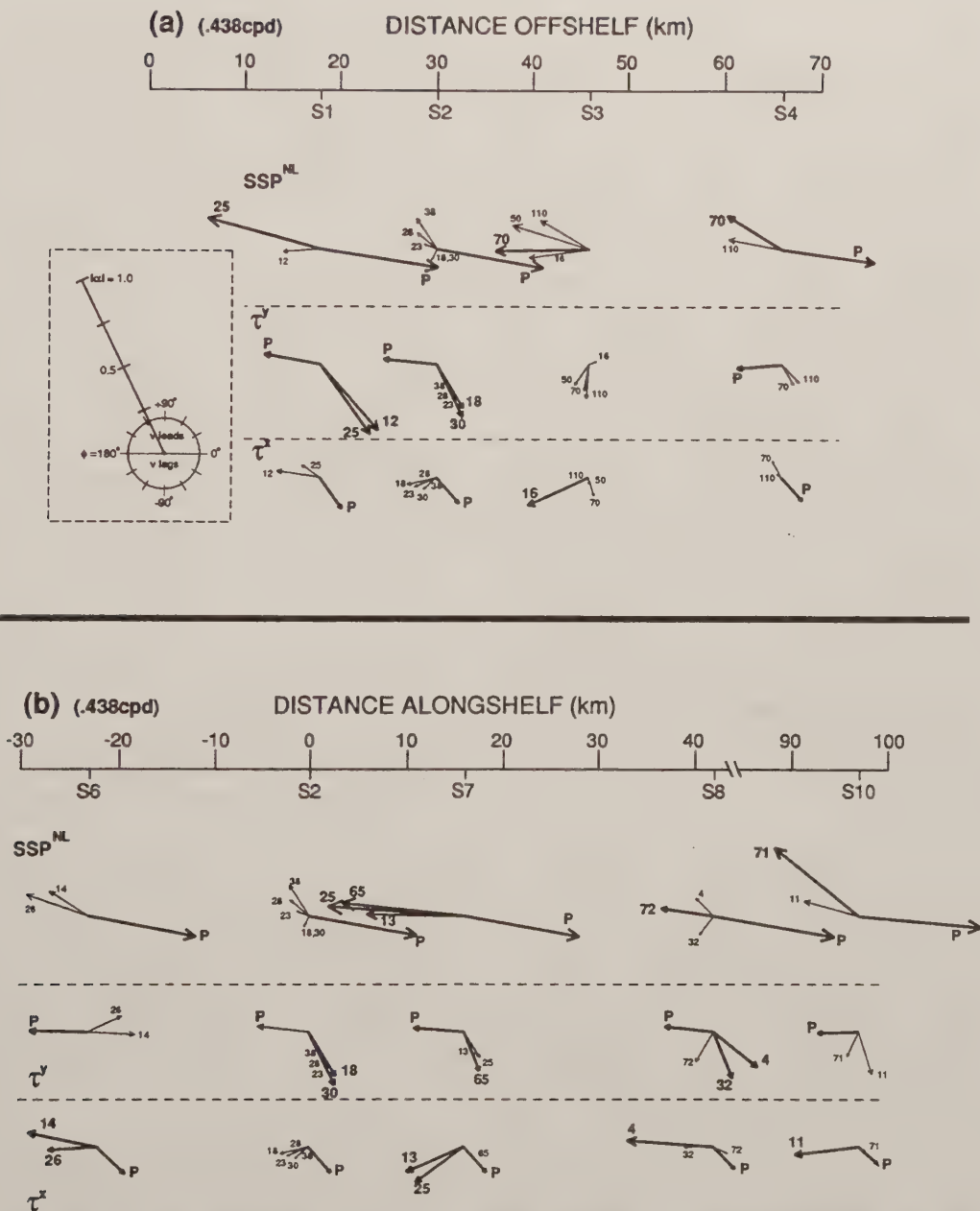


FIG. 9. Response of low-passed alongshelf current at 0.438 cpd to the forcing terms SSP^{NL} , τ^y , and τ^x in the statistical model (1) for stations in the (a) Halifax line and (b) 100-m isobath line. Vectors describe amplitude and phase of response (bold vectors and depth values denote 95% significance). SSP results from Schwing (1989), denoted by P , included for reference.

little consistent change in $|\alpha|$ or ϕ_α along the 100-m isobath is observed (Fig. 9b).

The response amplitude to τ^x in the surface layer is

typically $0.3 \text{ m s}^{-1}/\text{Pa}$. Little response of v to cross-shelf wind stress is seen at depths greater than 50 m. Wright et al. (1986) observed this pattern off south-

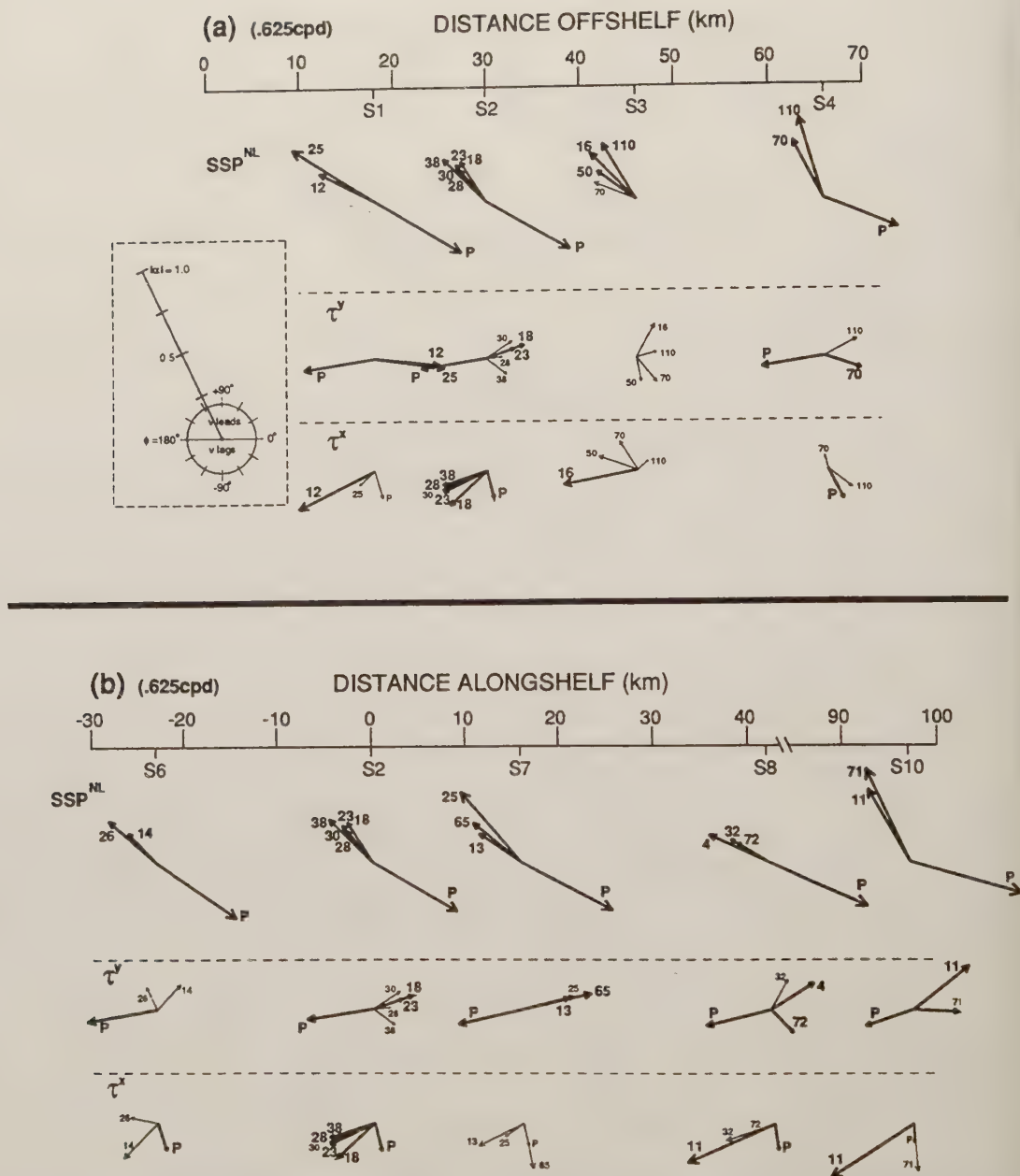


FIG. 10. Response of low-passed alongshelf current at 0.625 cpd to the forcing terms SSP^{NL} , τ^y , and τ^x in the statistical model (1) for stations in the (a) Halifax line and (b) 100-m isobath line. Vectors describe amplitude and phase of response (bold vectors and depth values denote 95% significance). SSP results from Schwing (1989), denoted by P , included for reference.

western Nova Scotia as well. Near-surface v is approximately out of phase with τ^x , consistent with a flow to the west (east) due to an offshore (onshore) wind stress.

As with the transfer functions, the dominant feature in R^2 and percent variance results is the lack of any defined trend (Fig. 11). In contrast to nearly constant

R^2 values for SSP at all frequencies, R^2 values at 0.438 cpd relative to 0.125 cpd vary greatly by station. Here R^2 appears to be related directly to the contribution from remote forcing, which accounts for a maximum of 50% but typically less than 25% of v variance. These results also suggest the reduced role of SSP^{NL} in the synoptic band. The percentage attributed to τ^y decreases noticeably with distance offshore but remains constant alongshelf.

The contribution of τ^x , however, varies greatly from station to station and decreases with depth. Stations where the response to τ^x is greatest, also where an anomalous amount of variance is explained by cross-shelf wind stress (S3, S8, S10), were located in the axis of the Nova Scotia Current (Anderson and Smith 1989). This trend is also seen at higher frequencies. Thus, variations in the intensity or position of this current at these frequencies may be controlled by τ^x .

The amplitudes of v contributed by local and non-local effects are more comparable than those seen at lower frequencies, primarily because the nonlocal gain is reduced by a factor of 3 or more in the synoptic band. The magnitude of the nonlocally forced alongshelf current is ~ 0.6 – 1.3 cm s^{-1} , versus ~ 1 – 2 cm s^{-1} for τ^y and ~ 1 cm s^{-1} for τ^x .

c. $\omega = 0.625$ cpd

Responses at frequencies higher than the synoptic band, as exemplified by the results at 0.625 cpd (Fig. 10), are very similar in magnitude to those at 0.438 cpd. The $|\gamma|$ values are 0.25 – 0.50 $\text{m s}^{-1}/\text{m}$ and exhibit little cross-shelf change (Fig. 10a), but tend to decrease to the west (Fig. 10b). The phase lead of v over SSP^{NL} decreases with distance offshore. Again the phase of the SSP response is consistent with a strongly frictional, geostrophic balance between v and η_x .

Unlike the lagged response of v to τ^y observed at lower frequencies, statistically significant ϕ_α values in the surface layer at 0.625 cpd are close to 0° . Thus, at sufficiently high frequencies the alongshelf wind-forced response appears to be frictionally dominated. Here v lags τ^x by 150° – 160° , similar to 0.438 cpd, such that alongshelf current leads cross-shelf wind stress by 2–3 h. Again there is some evidence of a decrease in $|\beta|$ with depth.

The R^2 values are of similar range (0.4–0.8) as those at other frequencies, and again are smaller than associated coherences in the SSP signal (Fig. 11). In general, the importance of nonlocal forcing is smaller at higher frequencies, while the role of τ^x seems to be greater in, but confined to, the near-surface layer.

Because the variance of Louisbourg SSP does not drop off at $\omega > 0.5$ cpd, while wind stress variance is greatly reduced at these frequencies (Fig. 7b), the ratio of the remote to local current at 0.625 cpd is large relative to the synoptic band. The amplitude of v associated with SSP^{NL} and τ^y is about 0.6 – 1.2 cm s^{-1} , compared to the τ^x contribution of 0.5 – 0.9 cm s^{-1} .

5. Discussion

As discussed in the Introduction, Scotian Shelf SSP is effectively accounted for by a statistical model that includes local and remote forcing (Schwing 1989). The response of the pressure field to wind stress and non-local effects is also physically meaningful. These features stand in contrast to the subinertial current response described previously, with its reduced correlations and sizable variability from station to station. Some patterns in the velocity response are reflected in the SSP behavior. Alternatively, the relatively poor statistical results and differences between the v and SSP responses suggest additional dynamical processes that may profoundly influence circulation, yet are unaccounted for by simple dynamical models, such as those applied by Csanady (1978) and Schwing (1989).

The most obvious similarity between alongshelf velocity and SSP is in their remotely forced (free) contributions. The amplitudes of the response of both parameters typically decay to the west and offshore. Changes in phase generally imply a propagation to the west, consistent with the direction of freely propagating CTWs. However, the phase speed in the velocity signal is difficult to determine with statistical certainty, given the generally large confidence intervals and the relatively small spatial extent of the mooring array.

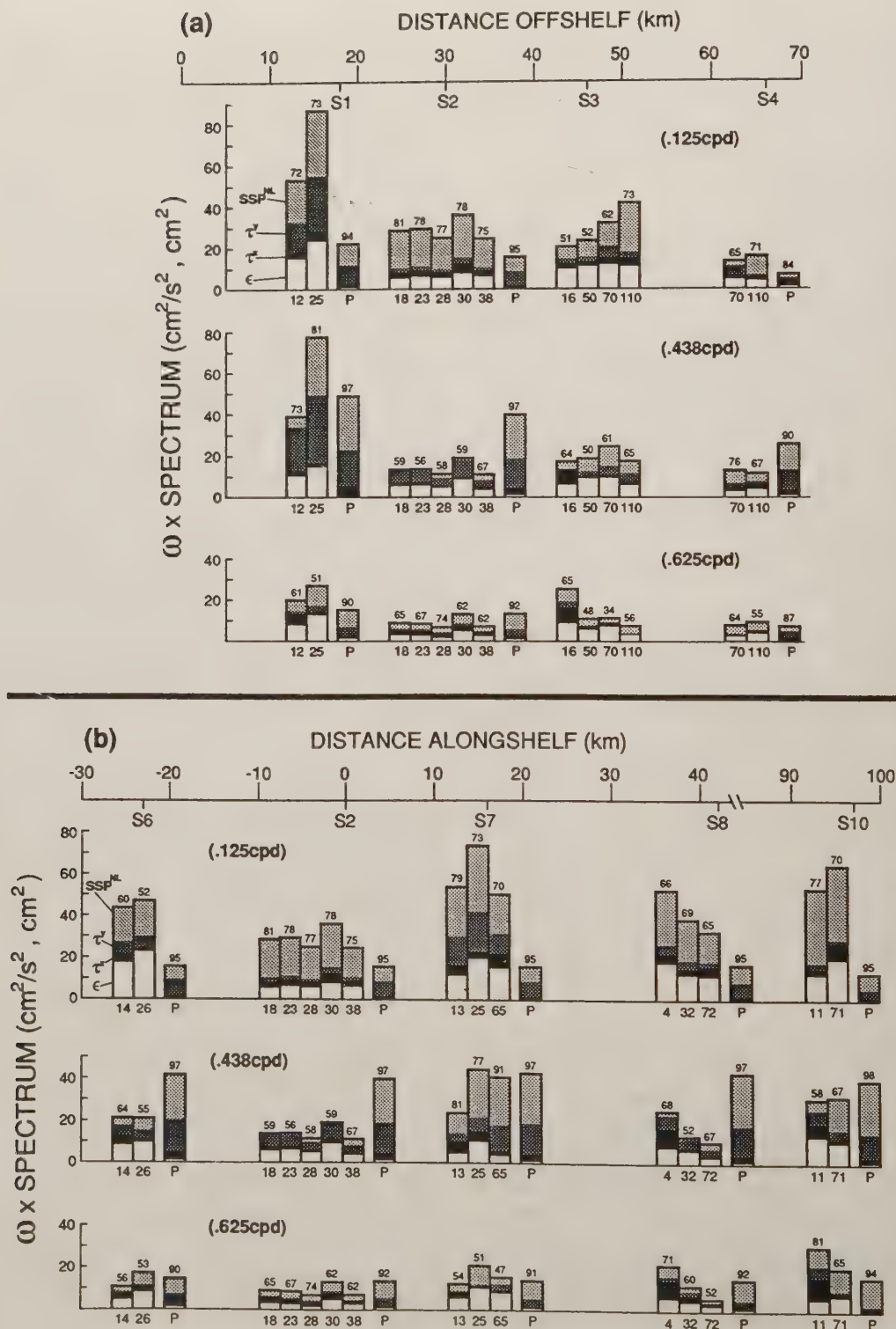
A comparison of the v and SSP responses to remote forcing at any mooring reveals that the two signals are approximately out of phase at all frequencies (Figs. 8–10). A simple geostrophic balance gives the alongshelf barotropic transport through the Halifax line provided

$$\Delta\eta = \frac{f}{g} \int_0^{x=SS} \bar{v} dx, \quad (2)$$

where $\Delta\eta$ is the difference between the nonlocal SSP response at S5 and Sambro (at the coast), and $\bar{v}$ is the depth-averaged alongshelf current response for the significant results presented in Figs. 8–10. A comparison of $\Delta\eta$ to $\hat{\Delta}\eta$, an estimate of the cross-shelf pressure gradient based on the averaged current gain at S1–S4 [rhs of (2)] demonstrates that the remote response is primarily geostrophic (Table 1). The estimate of the cross-shelf pressure gradient is poorest at 0.125 cpd.

A geostrophic balance between the local wind-forced current and SSP is tested as well. Applying (2) to the τ^y response suggests the wind-forced alongshelf current is balanced by the pressure gradient at $\omega > 0.2$ cpd. Like the remote response, however, transport at the lowest frequencies overestimates the gradient. Thus, quasi-steady motions appear to involve a more complex set of dynamics.

The data described here are consistent with other results suggesting that the Scotian Shelf response is largely wind driven (Petrie and Smith 1977; Smith et al. 1978; Sandstrom 1980; Schwing 1989). A comparable set of response functions was determined from velocity records obtained off southwestern Nova Scotia,



west of the CASP array (Wright et al. 1986). Quasi-steady alongshelf current gains to alongshelf wind stress at Sable Island are $0.5\text{--}0.75\text{ m s}^{-1}/\text{Pa}$, based on three moorings inside the 100-m isobath. This response is very similar to that seen at S1 at 0.125 cpd (Fig. 8a). The amplitudes of the nearshore current responses are also reasonably consistent with the steady numerical model results of Wright et al. Preliminary analysis of the current observations off southwest Nova Scotia, using the multiple regression model applied to the CASP records, has given results consistent with the locally and remotely forced time-dependent results described here (P. C. Smith, personal communication).

Wright et al. (1986) also clearly demonstrate the importance of a properly prescribed sea level condition at the backward (eastern) boundary of their model. A setup in coastal pressure at that boundary, which presumably represents the effect of wind stress integrated over the backward portion of the shelf, is required to properly estimate the observed current gains. This setup can be thought of as the remote contribution to the total flow, consistent with the statistical approach used here. The SSP and current gains calculated in the previous section also suggest that the magnitude of the coastal setup applied by Wright et al. is reasonable.

The importance of cross-shelf wind stress forcing of v during CASP was confined near the surface, particularly in the synoptic band. Wright et al. (1986) observed a similar pattern. Such results suggest that contributions from τ^x are primarily in the form of a near-surface (possibly Ekman) flux alongshelf, somewhat reduced relative to the alongshelf flow due to τ^y . A similar relationship between τ^y and u may exist. However, nearly all cross-shelf current responses are too small to be presented with statistical certainty. Cross-shelf flux time series are neither visually nor statistically coherent.

Features of the meteorologically forced circulation of the Scotian Shelf are also consistent with observations from adjacent shelf areas. Flow on the Labrador (Webster and Narayanan 1988) and Newfoundland (Greenberg and Petrie 1988) shelves is generally parabolic, but also features substantial mesoscale variability. Wright et al. (1987) and Webster and Narayanan (1988) conclude that nonlocal forcing, probably originating from Hudson Bay, is a major contributor to the flow. Noble et al. (1983) found 75%–90% of low-frequency alongshelf current variance on Georges Bank and in the Middle Atlantic Bight, west of the Scotian Shelf, is due to the combined effects of local wind forcing and free propagations. Ou et al. (1981) reached a similar conclusion for the Middle Atlantic Bight. The relative contribution of these sources of

TABLE 1. A comparison of the cross-shelf difference in the amplitude of the SSP response to SSP^{NL} and τ^y . The terms $\Delta\eta$ are the differences in the response of SSP at Sambro and S5 (taken from Schwing 1989) for three representative frequency bands. $\hat{\Delta}\eta$ values are estimates of this difference found by integrating the appropriate depth-averaged alongshelf current responses at S1–S4, based on the geostrophic balance $\eta_x = (f/g)v$.

$\omega(\text{cpd})$	Nonlocal (SSP^{NL}) ($\text{m s}^{-1}/\text{m}$)		Local (τ^y) ($\text{m s}^{-1}/\text{Pa}$)	
	$\Delta\eta$	$\hat{\Delta}\eta$	$\Delta\eta$	$\hat{\Delta}\eta$
.125	.55	.85	.19	.34
.438	.25	.27	.20	.21
.625	.30	.31	.24	.20

variability varies with location; remote forcing is relatively more important on Georges Bank. Thus, the idea of separating the circulation into local and remote portions is valid in regions adjacent to the Scotian Shelf.

The discrepancy between the spatial coherence scales of SSP and current described here is similar to the results of Vermersch et al. (1979) for the Gulf of Maine. While the winter pressure field is highly coherent over the entire gulf, the horizontal coherence scale of the velocity field is less than 50 km and current is poorly correlated with local wind. Vermersch et al. speculate that the gulf's very rough bathymetry is responsible for generating mesoscale eddies. The results of Webster and Narayanan (1988) suggest that bathymetric irregularities also lead to significant variations in flow on the Labrador Shelf. The dominant bathymetric scales of these two regions are quite similar to those of the CASP study area; thus, the idea of bathymetrically influenced flow on the Scotian Shelf is worth considering and is pursued in the numerical study that follows (Schwing 1992).

Because the wind-forced responses observed in this study are small and associated confidence intervals are large, it is difficult to estimate the phase speed at which locally forced features propagate through the current array. However, the strongest response to τ^y (at 0.438 cpd) suggests an alongshelf phase propagation to the west, consistent with the SSP response. Thus, gross features of the forced and free current response can be accounted for by similar physically intuitive models (cf. Csanady 1978; Schwing 1989). However, mesoscale variations in the velocity field that do not appear in the SSP signals must develop in response to either 1) a more complex set of physics or 2) a complex bathymetry or wind field that does not affect pressure to nearly the same degree.

FIG. 11. (a) Percentage of low-passed alongshelf current variance due to each of the forcing terms (SSP^{NL} , τ^y , and τ^x), and model error in the statistical model (1), for stations in the (a) Halifax line and (b) 100-m isobath line. Height of each histogram bar denotes total current variance (variance preserved) at the depth given below each bar. Total percentage of variance explained by the model given above each bar. SSP results from Schwing (1989), denoted by P , included for reference.

Current observations typically are associated with smaller dominant length scales than are SSP observations (cf. Rhines 1977, pp. 196–202). Willebrand et al. (1980) have shown that spatial inhomogeneities in wind or bathymetry can cause wind and current signals to become incoherent. The SSP can be thought of as an integral measure of the flow. Thus, it is analogous to a spatially filtered representation of the circulation, in which variations due to wind stress or bathymetry on subsynoptic horizontal scales are removed. For a spatially uniform wind or bathymetry, the velocity field is fairly homogeneous and would be changed little by this “filtering” process; thus, velocity and SSP coherence scales are similar. However, as the dominant scales for wind stress or bathymetry decrease, so do those for the circulation. In the case of a spatially complex depth or wind field, pressure—the integral representation of the flow—is strongly incoherent with velocity.

Finally, it is important to note that the horizontal extent of the CASP instrument array was small relative to those of wind-forced and free circulation features. These small distances, and the relatively large confidence intervals, point to the need for a spatially more extensive current meter and bottom pressure array to confidently replicate the scales of the locally and nonlocally forced responses detected in the coastal SSP records (Schwing 1989). The ongoing analysis of current meter records obtained over the western portion of the Scotian Shelf, off West Head (Fig. 1), using the multiple regression model applied here (P. C. Smith, personal communication) will hopefully shed some light on this issue.

6. Summary

Two primary current regimes exist on the portion of the Scotian Shelf covered by the CASP mooring array. Flow inside the 100-m isobath is rectilinear and parallel to the general bathymetry. Although the record mean is nearly zero, the predominantly alongshelf current oscillates at periods of 2–5 d in response to local wind forcing over the shelf. Maximum velocities of $0.2\text{--}0.3\text{ m s}^{-1}$ were recorded in this nearshore region. The current at offshore moorings features a mean westward velocity of about 0.3 m s^{-1} , although a meteorological response at synoptic frequencies is again observed. The time-varying portion of velocity in both regions is generally uniform with depth. Anderson and Smith (1989) conclude that the mean circulation during CASP was predominantly barotropic. The results of Lively (1988) suggest the flow is largely barotropic at synoptic periods as well, particularly in the near-surface layer and throughout the inner portion of the shelf. However, the potential importance of baroclinicity cannot be completely ignored on the outer shelf.

In contrast to the highly coherent response of SSP to local and remote forcing, the velocity response, obtained with a multiple regression model that includes

local and nonlocal effects, exhibits substantial variability from station to station, and is not nearly as coherent with wind stress. Nonlocal forcing dominates at $\omega < 0.2$ cpd, while local wind and remote contributions are similar at higher frequencies. Cross-shelf forcing has more effect on current than SSP, but its influence is limited to the near-surface layer. The total velocity variance explained with this model is about 40%–80%, and is generally highest at the shallow stations.

Both velocity components exhibit regions of flow that are poorly correlated with local and remote forcing, vary without pattern in space, and are generally inconsistent with SSP results. If averaged over the mooring array, the statistical results suggest that many of the current patterns are also observed in SSP data, and can be related to physically meaningful concepts. For example, CTW activity is suggested by characteristics of the velocity and SSP response to remote forcing. The current response to local and remote forcing integrated across the Halifax line is consistent with the geostrophic flow estimated from the SSP response; thus, the large-scale current can be determined from the pressure field. However, velocity variations on scales of 10–100 km are not reflected in the SSP signal, which implies that the rugged bathymetry of the Scotian Shelf may induce modifications in the circulation that are not manifested in the SSP records.

In a companion paper (Schwing 1992), a numerical model is developed and applied to the problem of wind-forced flow over irregular bathymetry. Two particular questions will be explored. First, how and to what degree do bathymetric variations, like those seen on the Scotian Shelf, influence locally and remotely forced circulation patterns? Second, how are these perturbations reflected differently in SSP and velocity? It is hoped that model results will explain the discrepancies between the highly coherent SSP response and the irregular velocity response, as detailed here.

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Subtidal Response of Scotian Shelf Circulation to Local and Remote Forcing. Part II: Barotropic Model

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ABSTRACT

A linear, barotropic numerical model that features realistic bathymetry of the Scotian Shelf provides solutions forced by steady and periodic wind stress that are generally incoherent on spatial scales of the shelf width. Closed circulation cells occur in association with, and on the scales of, major bathymetric features. Bathymetrically steered flow is prevalent, and more evident at lower frequencies. Model transport forced by a coastally trapped wave propagating across the backward boundary is not sensitive to the modal structure of the incident wave; bathymetry rapidly modifies the wave form as it propagates in the free direction. Higher modes and reflected waves are probably dissipated over short distances by scattering and strong bottom stress. Patterns seen in the model solutions are consistent with results from more fundamental models, and are readily explained by relatively simple vorticity balances.

Model results generally reproduce the diverse local and nonlocal velocity responses observed on the Scotian Shelf during winter. The model is more effective in accounting for the remote contribution to circulation. Wind-forced results generally reflect the observed directional variability, and are similar in magnitude to observations inside the 100-m isobath but underestimate the actual current response at deeper stations. It is speculated that spatial variability in wind stress, an effect not addressed in this work, may be responsible for some of this difference. The significance of baroclinic effects in deeper water, which cannot be discounted, is also beyond the scope of this model. Nevertheless, the fairly good agreement between the model and observed current responses to local and nonlocal forcing confirms the importance of bathymetric modifications to Scotian Shelf circulation at subtidal frequencies.

1. Introduction

Winter storms crossing the coastal region of eastern Canada generate a systematic, well-defined response in subsurface pressure (SSP) on the continental shelf. Observations from the Canadian Atlantic Storms Program (CASP) on the Scotian Shelf show that over 90% of the subtidal energy in the SSP field is attributable to a combination of direct forcing by local wind stress and remote forcing by coastally trapped waves (CTWs) (Schwing 1989a,b). The SSP is set up (down) by the predominantly alongshelf stress to the east (west) in a response that is strongly coherent over the entire shelf. The magnitude of the locally forced response increases to the west (the forward or free direction) as the response diffuses away from the coast, consistent with Csanady's (1978) arrested topographic wave (ATW) theory. Changes in phase suggest propagation of the locally forced SSP signal to the west. Solutions to a harmonic time-dependent form of this model agree quite closely with the CASP observations (Schwing

1989b). The nonlocal contribution to SSP propagates and decays offshore and to the west, in quantitative agreement with frictional CTW theory for idealized Scotian Shelf bathymetry. The importance of remote forcing relative to local stress decreases to the west, as CTW modes are reflected, scattered, and frictionally decay while the local response grows in the forward direction.

However, subtidal current fluctuations on the Scotian Shelf are less coherent in space, and with local and remote meteorological forcing (Schwing 1989a, 1992). The large-scale observed current response reflects some of the features noted in the SSP field, although considerable variations occur within the mooring array on horizontal scales of less than 100 km. The discrepancy between the velocity and SSP coherence scales is similar to that observed by Vermersch et al. (1979) in the nearby Gulf of Maine. They suggest that mesoscale variations in bottom bathymetry, similar to those occurring on the Scotian Shelf, induce current variability on the same scale. Webster and Narayanan (1988) attribute differences between model results and observations on the Labrador Shelf to bathymetric irregularities.

Numerous idealized analytical (Csanady 1974; Wilkin and Chapman 1987; Middleton and Wright

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1988) and numerical (Wang 1980; Simons 1983; Brink 1986; Haidvogel and Brink 1986; Wilkin and Chapman 1990) studies have demonstrated a link between complex circulation features and bathymetric structures. Other theoretical studies that considered more realistic bottom geometries display a similar flow/bathymetry relationship (Hsueh 1980; Beardsley and Haidvogel 1981; Hopkins and Dieterle 1983; Wright et al. 1986; Greenberg and Petrie 1988; Lynch et al. 1992). A series of simple analytical and numerical model simulations by Schwing (1989a) demonstrate that a highly variable velocity field develops over irregular bathymetry, primarily because of small-scale circulation features created by bathymetric steering, vortex stretching, and the scattering of wave energy by bathymetric features. The velocity response observed during CASP cannot be reconciled with the simple model applied to SSP (Schwing 1989b).

To relate these fundamental model results back to the CASP observations detailed in Schwing (1992), numerical techniques are applied here to the problem of locally and remotely forced flow on the Scotian Shelf, using actual bathymetric data for the region. Solutions are compared with observations to verify how well these models explain the balance of forces that control subtidal flow, with emphasis on the role of complex bathymetry. Model results for idealized bathymetric examples will aid in the interpretation of the more realistic case studies described here. In addition, model results from remote portions of the Scotian Shelf will serve as a reference frame for future observational studies. Finally, it is hoped that these results will provide further insight on the proper remote forcing for Gulf of Maine, Georges Bank, and Middle Atlantic Bight models. Chapman et al. (1986) conclude that the observed mean flow in the Middle Atlantic Bight may be driven strictly by inflow from the Scotian Shelf.

In section 2, the numerical model is derived, and the bathymetric mesh and boundary conditions for the Scotian Shelf models are described. Model results forced by wind stress over the shelf are presented in section 3. The nonlocal contribution, driven by a CTW incident at the backward (eastern) cross-shelf boundary, is discussed in section 4. The observed velocity response to these sources of energy, discussed in Schwing (1992), is compared to model currents as well. A discussion of these results, and their limitations, follows in section 5.

2. The numerical model

a. Derivation of the governing equation

A governing equation is sought in terms of sea surface elevation η from the two-dimensional linear, shallow-water, barotropic equations of motion and continuity:

$$i\omega u - fv = -g\eta_x + \frac{\tau^x}{h} - \frac{ru}{h} \quad (1)$$

$$i\omega v + fu = -g\eta_y + \frac{\tau^y}{h} - \frac{rv}{h} \quad (2)$$

$$i\omega\eta + (uh)_x + (vh)_y = 0, \quad (3)$$

where u , v are depth-averaged cross-shelf (x) and alongshelf (y) components of velocity, respectively; τ^x , τ^y are kinematic wind stress components in the cross- and alongshelf directions, respectively; f is the (constant) Coriolis parameter; g is the acceleration due to gravity; h is the water depth; and r is the linear bottom stress coefficient. Subscripts denote partial differentiation. The right-handed coordinate system (Fig. A1) defines $x = 0$ at the coast and increasing offshore; y becomes increasingly negative in the direction of free wave propagation (i.e., forward). Harmonic time dependence of the form $e^{i\omega t}$ is assumed for all time derivatives, where ω is the frequency of forcing.

Equations (1)–(2) give equations for the current components

$$u = \frac{1}{1 + \epsilon^2} \left[-\frac{g}{f} (\epsilon\eta_x + \eta_y) + \frac{1}{fh} (\tau_y + \epsilon\tau^x) \right] \quad (4)$$

$$v = \frac{1}{1 + \epsilon^2} \left[\frac{g}{f} (\eta_x - \epsilon\eta_y) + \frac{1}{fh} (\epsilon\tau^y - \tau^x) \right], \quad (5)$$

where

$$\epsilon = i\frac{\omega}{f} + \frac{r}{fh}. \quad (6)$$

Now substituting (4)–(6) into (3) yields the governing equation

$$\begin{aligned} \frac{a^2\epsilon}{1 + \epsilon^2} (\nabla^2\eta) + \left[\left(\frac{a^2\epsilon}{1 + \epsilon^2} \right)_x - \left(\frac{a^2}{1 + \epsilon^2} \right)_y \right] \eta_x \\ + \left[\left(\frac{a^2}{1 + \epsilon^2} \right)_x + \left(\frac{a^2\epsilon}{1 + \epsilon^2} \right)_y \right] \eta_y - i\frac{\omega}{f} \eta \\ = \frac{1}{f^2} \left[\left(\frac{\tau^y + \epsilon\tau^x}{1 + \epsilon^2} \right)_x + \left(\frac{\epsilon\tau^y - \tau^x}{1 + \epsilon^2} \right)_y \right], \quad (7) \end{aligned}$$

where $a^2 = gh/f^2$. Equation (7) is an elliptic partial differential equation expressed solely in terms of the variable η , but is not readily solved with analytical techniques. Various assumptions and approximations may be applied to (1)–(3) to reduce (7) to an equation that can be solved analytically (cf. Wilkin and Chapman 1987; Middleton and Wright 1988).

Alternatively, a numerical approximation can be applied. The discretization of (7), and its solution using successive overrelaxation (SOR), a point-iterative, explicit method (Young 1971, p. 73ff.; Press et al. 1986, pp. 652–659), is discussed in appendix A. An advantage of relaxation schemes over other numerical techniques is that the matrix of coefficients **A**, given by (A4), is not altered during computations. Thus, the problem of accumulation of round-off errors experi-

enced by many direct methods, such as Gaussian elimination, can be avoided. SOR is also extremely efficient because 1) only nonzero values of $\mathbf{A}$, a very small percentage of the elements, are stored, 2) values of the solution are updated in place, as they become available during the iteration, and 3) a relaxation parameter α is applied to overcorrect, in the case of $\alpha > 1$, the initial solution, which leads to more rapid convergence to the final solution (Young 1971, pp. 73–74). The convergence rate for SOR provides three-figure accuracy after about N iterations, where N is the number of model elements. Details of the discretization scheme are given in Fig. A1.

b. The model bathymetry

Model bathymetry (Fig. 1), supplied by Sylvain de Margerie (ASA Consulting, Ltd., Halifax, Nova Scotia), was developed from a database of existing depth soundings for the Scotian Shelf and adjacent areas. Observations were averaged into 10-km by 10-km elements. The coastline was smoothed to simplify the boundary, the coastal depth was set to 10 m, and land

regions were masked. The cross-shelf resolution was then doubled to 5 km by interpolation. The final bathymetric dataset used in the numerical model contains 59 points cross-shelf and 88 values alongshelf, corresponding to a 290- by 870-km domain. Major bathymetric features and the approximate locations of CASP stations are indicated in Fig. 1.

The backward (relative to the direction of free wave propagation) cross-shelf boundary ($y = 150$ km) was set to the exponential form

$$h(x) = h_L \exp[2b(x - L)]$$

over the region $0 < x < L$, where $h_L = 200$ m, $bL = 0.35$, and $L = 230$ km, the approximate offshore position of the 200-m isobath in this region. These depths were smoothed linearly into the actual bathymetry at the origin (Louisbourg), over the alongshelf distance $0 < y < 150$ km. The cross-shelf structure of any CTW mode can be determined analytically for the profile at this boundary (cf. Wilkin and Chapman 1987; Middleton and Wright 1988), as described in appendix B. The incident wave then adjusts to the actual bathymetry over the "patched" section east of Louisbourg. This patched region is rather complicated in reality. However, the model is not sensitive to the form of bathymetric transition, and the model circulation in this region is not crucial to the interpretation of the CASP observations.

Finally, the depth matrix was smoothed with a weighted 3×3 spatial filter:

$$h_{i,j}^{\text{smoothed}} = (h_{i+1,j} + h_{i+1,j+1} + h_{i,j+1} + h_{i-1,j+1} + h_{i-1,j} + h_{i-1,j-1} + h_{i,j-1} + h_{i+1,j-1} + 5h_{i,j})/13,$$

where the subscripts denote the mesh point, as defined in Fig. A1. The filter was applied three times to interior points in the matrix. Some areas were further smoothed to avoid model instabilities where the depth gradient is too severe, given the $\Delta x = 5$ km cross-shelf and $\Delta y = 10$ km alongshelf interval between mesh points.

c. Boundary conditions

Along the coastal boundary ($y > -570$ km, Fig. 1), transport normal to the coast must be zero. The condition at mesh points where the coastline is oriented parallel to the y axis is obtained from (4), assuming $uh_0 = 0$, where h_0 is the nonzero depth and ϵ_0 is ϵ , evaluated at the coast:

$$\eta_x + \epsilon_0^{-1} \eta_y - \frac{\tau^x}{gh_0} - \frac{\tau^y}{\epsilon_0 gh_0} = 0. \quad (8a)$$

At coastal points where the coastline orientation is parallel to the x axis, the requirement that $vh_0 = 0$ is combined with (5) to give

$$\eta_y - \epsilon_0^{-1} \eta_x + \frac{\tau^x}{\epsilon_0 gh_0} - \frac{\tau^y}{gh_0} = 0. \quad (8b)$$

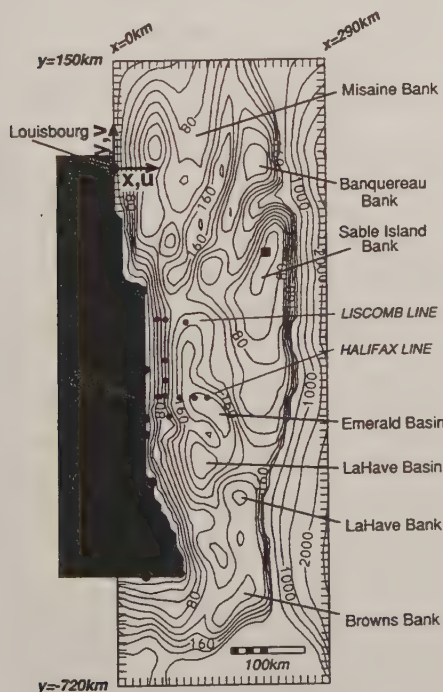


FIG. 1. Domain and bathymetry used in Scotian Shelf numerical model simulations. Model mesh is 290 km wide and 870 km in length. The 10-km resolution is denoted by the tick marks. Approximate position of Nova Scotia shown by shaded area. Location of major bathymetric features is indicated. Approximate position of CASP coastal and offshore stations denoted by solid circles. Larger circle denotes Louisbourg (model origin). Square denotes location of Sable Island meteorological station.

All the terms in (8) are of similar order for typical coastal depths $h_0 = O(10 \text{ m})$. Csanady (1980) elaborates on this condition, and justifies the need for $h_0 \neq 0$.

The offshore alongshelf boundary condition

$$\eta = 0 \quad (9)$$

is applied seaward of the 200-m isobath at the shelf break. It is based on the assumption that synoptic variations in η over the continental slope and deeper regions are negligible (Beardsley and Haidvogel 1981; Wright et al. 1986). Transport onto the shelf must be conserved. To compensate for the large decrease in depth, the depth-integrated cross-isobath velocity must be small compared to u on the outer shelf. Since flow in the deep ocean is nearly geostrophic, $\eta_y \approx 0$ at the ocean boundary and η can be approximated as a constant (Hsueh 1980; Beardsley and Haidvogel 1981; Hopkins and Dieterle 1983; Wright et al. 1986).

This assumption eliminates the need for computations in the shelf slope region, where the depth gradient is too severe to allow stable solutions given a mesh size sufficiently large to keep computing times at a reasonable length. Results from sensitivity studies, using various idealized forms of bathymetry in the offshore region and applying condition (9) at the outer alongshelf boundary of the domain, suggest that prescribing sea level to zero along the shelf break has only minor effects on shelf SSP and transport. Furthermore, these effects are confined to within a few mesh points of the break.

Hsueh (1980) and Hopkins and Dieterle (1983) discuss some of the limitations of this approximation. Hopkins and Dieterle treat the distribution of η_y , necessary to solve the backward boundary condition, as the sum of two gradients that decay away from the coast and the shelf break. These can be thought to be forced by local wind stress and the deep ocean, respectively. The total shelf circulation therefore could be separated into three contributions: local wind forcing and remote forcing across the backward boundary, as applied here, plus remote forcing from offshore. The effects of the last component are beyond the scope of this study, but are probably minimal. Chapman et al. (1986) conclude that relatively little exchange occurs across the shelf break in the area just west of the Scotian Shelf.

The condition

$$\eta_{yy} = 0 \quad (10a)$$

applied at the forward (relative to the direction of free wave propagation) cross-shelf boundary ($y = -720 \text{ km}$) allows flow out of the domain to compensate for mass divergence in the interior (Hsueh 1980; Hopkins and Dieterle 1983). A concern of those studies is that (10a) may be overprescribed if the second derivative of η is small throughout the interior. Given the short bathymetric scales in y on the Scotian Shelf, however, this condition is appropriate. Similarly,

$$\eta_{xx} = 0 \quad (10b)$$

is applied along the open portion of the $x = 0$ boundary west of Nova Scotia; that is, $y < -570 \text{ km}$ (Fig. 1).

Before describing the backward cross-shelf boundary conditions for the local and remote models, an explanation of how they were treated is in order. Schwing's (1992) analysis of the CASP observations separates the circulation into locally and remotely forced portions, based on a concept suggested by Gill and Schumann (1974) and others (cf. Lopez and Clarke 1989). The locally forced contribution is due to wind stress over the Scotian Shelf and, by definition, must be zero at some cross-shelf section near the eastern edge of the shelf. The structure of η at the origin ($y = 0$) represents the accumulated transport onto the Scotian Shelf, and is a function of the forcing and bathymetric conditions in the backward region (Hopkins and Dieterle 1983). For the Scotian Shelf model, I prescribe $\eta = 0$ at Louisbourg, near the Laurentian Channel (Fig. 1), an appropriate condition if little wind-forced variation in SSP traverses this deep channel. The remote portion of velocity is defined by the total SSP signal measured at Louisbourg, regardless of its source and structure. Another physical interpretation of this solution is that the remote contribution is due to a (primarily low-mode) pressure gradient force, while the local (higher-mode) response is dependent on direct wind stress (Lopez and Clarke 1989).

Since η must match at the junction of the offshore and cross-shelf boundaries, condition (9) is also applied at $y = 0$ for the periodic wind-forced cases (section 3). This is a critical prescription, as it assumes the SSP signal at this boundary is associated solely with motions generated remote from the shelf. As Wright et al. (1986) have pointed out, the observed response is highly sensitive to changes in this condition. Thus, solutions to (7) subject to (9) at $y = 0$ represent only that portion of SSP forced by local wind stress (i.e., directly over the model domain); nonlocally generated motions are excluded from the solution.

The nonlocal contribution to the circulation (section 4) is forced at the backward boundary ($y = 150 \text{ km}$) by a single-mode CTW. This condition is determined analytically by calculating the cross-shelf modal streamfunction for the exponential bottom profile (see appendix B). The cross-shelf structure of the incident wave, expressed in terms of η , is found by integrating the y -momentum equation (2) with respect to y , after substituting the constant Rayleigh damping coefficient $\lambda = r/h_0$ and the streamfunction Ψ (described in appendix B). Thus,

$$\eta(x) = \frac{f}{gh} \left[\Psi(x) + \frac{\epsilon}{il} \Psi_x(x) \right], \quad (11)$$

plus a constant of integration that reduces η to zero at the 200-m isobath to match (9) at the offshore boundary. Although the rigid-lid assumption is required to

obtain condition (11), it is relaxed in the interior of the model.

The numerical model was tested by forcing an incident low-mode CTW over various cross-shelf exponential, uniform alongshelf bathymetries. Solutions exhibited the phase speeds and exponential amplitude decay scales identical to analytical solutions of Eq. (B1) for the appropriate bathymetric scale and bottom friction coefficient (Schwing 1989a). Subsequent experience with the model (discussed in the following sections) revealed that the sea surface structure at the backward boundary is unimportant in model flow patterns over realistically complex bathymetry. The role of (11) is to force the model with a cross-shelf sea level setup, analogous to the remote contribution defined by Schwing (1992), and shown to be important by Beardsley and Haidvogel (1981), Chapman et al. (1986), Wright et al. (1986), and Lynch et al. (1992). It does not necessarily represent a CTW signal at Louisbourg, nor is it applied for the purposes of describing the remotely forced portion of the Scotian Shelf circulation in terms of a CTW modal structure.

The coastal (8), offshore (9), and forward (10) boundary conditions for the remotely forced problem are identical to those applied to the wind-forced case, although the wind stress terms in (8) are zero for the remote simulations. Sensitivity studies with a nonlocally forced streamfunction model using the cross-shelf radiation conditions for long and short CTWs (cf. Wang 1980) produced essentially identical results to that using (10)–(11).

Bottom stress is parameterized by setting it proportional to the depth-averaged velocity (Csanady 1980). The coefficient $r = 10^{-3} \text{ m s}^{-1}$ for all model results presented here, consistent with values derived empirically from observations and used in other shelf models (cf. Csanady 1978, 1982, pp. 185–186). Sensitivity studies indicate that this value of r provides the best reproduction of the SSP response at CASP coastal and mooring stations. These studies also show that decreasing r from 10^{-3} to $2 \times 10^{-4} \text{ m s}^{-1}$ raises the coastal SSP response by less than 20%, and has even less effect on the response farther offshore. The circulation features of note are not qualitatively affected by reasonable changes in r .

3. Model results for local wind stress forcing

a. Response to the mean wind field

The initial numerical model results are forced by a spatially uniform, steady ($\omega = 0$) wind stress over the entire domain (Fig. 2). The magnitude of the model stress is the record mean of the Sable Island wind stress time series during CASP; the alongshelf component ($\tau^y = 0.0436 \text{ Pa}$) dominates the cross-shelf contribution ($\tau^x = 0.0132 \text{ Pa}$). For clarity, all flow fields are presented at a 10-km resolution.

Transport near the coast is predominantly along isobath and toward the east. Although isobaths, hence transport, are generally parallel to the coast, even small bathymetric deviations can produce sizable cross-shelf flow. This is most apparent off Halifax, which is coincidentally very close to the CASP array (Fig. 1). Transport also generally increases in the direction of free wave propagation, consistent with the increased set-down of SSP seen in the CASP observations and idealized model results (Schwing 1989a,b), and according to ATW theory (Csanady 1978).

Transport near the eastern boundary and over the outer shelf banks (e.g., Sable Island Bank) is predominantly offshore, consistent with the direction of a surface Ekman flux for the mean wind. Compare the transport in these regions to that seaward of the 200-m isobath, where the current is solely a surface Ekman response.

Over the deeper portions of the outer shelf, however, the circulation is not nearly as simple. Flow through the saddle region separating Sable Island and La Have banks, and in the small canyon east of Sable Island, features a relatively strong *onshelf* transport that balances a large pressure gradient, despite the offshore favorable stress. These results suggest that slope water upwelled onto the shelf (Petrie 1983) may be transported into Emerald Basin during winter, even in the absence of stratification. Onshelf barotropic flow may account in part for the anomalously high proportion of intermediate slope water found during CASP within the deeper layers of Emerald Basin (Anderson and Smith 1989).

While transport is greatest through the aforementioned saddle region, the strongest depth-averaged velocity is generally confined inside the 100-m isobath and over Sable Island Bank (Fig. 2b). This is not surprising, since the response to surface and bottom stress is most efficient in the shallowest regions of the shelf.

The final noteworthy feature of the steady results is the existence of several circulation cells about 50–100 km in diameter, located in the deeper areas of the shelf where depth gradients are strongest (e.g., along the slopes of La Have Basin). These cells are very similar in appearance to those noted in idealized bathymetric cases, whose origin was shown to be due to vortex stretching (Schwing 1989a). The rather small horizontal coherence scales are also consistent with the time-dependent current patterns observed during CASP (Schwing 1992).

The mean flow displays features of the steady, wind-forced solutions for the Gulf of Maine numerical models of Wright et al. (1986) and Lynch et al. (1992), which include the western portion of the Scotian Shelf. Their results include the pattern expected by ATW theory, a strong tendency for flow along depth contours, and several areas of closed, bathymetrically controlled circulation. Both studies also noted transport into Northeast Channel, opposite the surface Ekman trans-

port but consistent with the winter observations of Ramp et al. (1986). Wright et al. determined that flow in this channel is nearly geostrophic. An analysis of the steady momentum balance near Sable Island Bank provides a similar conclusion.

b. Response to periodic wind stress forcing

Multiple linear regression models in the frequency domain were applied by Schwing (1989b, 1992) to determine the local and remote contributions to the circulation. The regression analysis separates the flow into a response to the two wind stress components, and to a nonlocally forced signal represented by Louisbourg

SSP. Model results presented in this section describe the velocity response to alongshelf and cross-shelf wind stress periodic at 0.125 and 0.438 cpd. The wind stress amplitude is 1 Pa over the shelf forward of Louisbourg, but zero in the region east of Louisbourg. Thus, numerical solutions can be compared directly to the statistical results from Schwing (1992), where the velocity signal at the cross-shelf transect off Louisbourg was defined as the nonlocal contribution to the flow.

Model transport forced by an alongshelf stress periodic at 0.125 cpd is presented at $t = 0$, when stress is at its maximum to the east (Fig. 3a), and at $t = \pi/2$, when the wind is relaxed after a half period ($-\pi/2 < t < \pi/2$) of eastward-directed stress (Fig. 3b). Transport

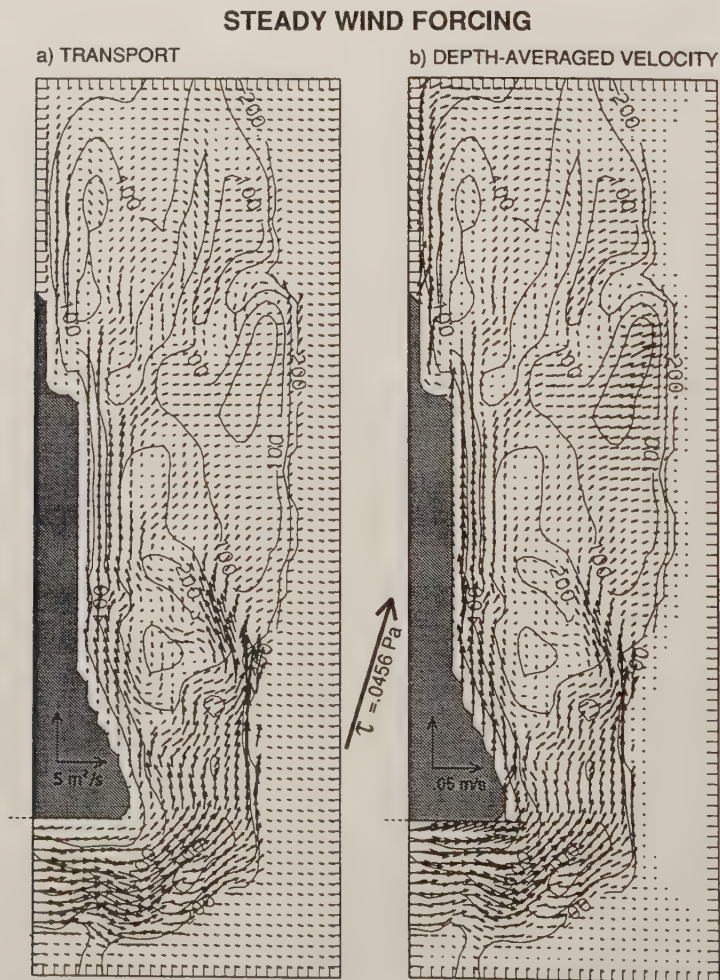


FIG. 2. Model circulation for Scotian Shelf, for mean wind stress during the CASP field deployment. Transport shown in (a); depth-averaged velocity shown in (b). Vector units are $\text{m}^2 \text{s}^{-1}$ and m s^{-1} , respectively. White areas denote velocity less than 0.0005 m s^{-1} .

amplitude is expressed in units of $\text{m}^2 \text{s}^{-1} / \text{Pa}$. The flow field at $t = 0$ looks much like that due to a steady wind stress (Fig. 2a), with significant variability on the horizontal scales of, and in association with, bathymetric features.

The weak transport in the region east of Louisbourg gives an indication of how rapidly reflected (short-wave) energy is dissipated over the rugged terrain of the Scotian Shelf. Bathymetry acts to reflect waves or scatter their energy into higher modes (Wang 1980; Wilkin and Chapman 1987, 1990; Middleton and Wright 1988). Realistic shelf geometries scatter significant levels of wave energy into higher modes (Wilkin and Chapman 1990). The resulting waves dissipate more rapidly than the forward-propagating incident wave (Schwing 1989a).

Since transport is nearly in phase with wind forcing, the flow is weak over most of the domain at $t = \pi/2$ (Fig. 3b). However, a rather substantial residual circulation exists in the two basins off Halifax, and over the western part of the shelf. As with the flow at $t = 0$ and the steady forcing case, mesoscale circulation features of order 100 km and less in diameter occur at several locations. Such features are intimately associated with bathymetric features having similar horizontal scales.

The amplitude of the current response to τ^x , the cross-shelf wind stress (Fig. 4), is smaller than the response to the alongshelf component of stress. Wright et al. (1986) also noted this in their (steady) Gulf of Maine model results. Since the winter wind on the Scotian Shelf is predominantly alongshelf, the contribution to the circulation by τ^x is minor. An offshore wind stress at $t = 0$ results in a generally westward transport (Fig. 4a), consistent with the surface Ekman flux produced by such a wind. Some bathymetric steering is again evident, although not to the same degree as was noted for the τ^y response. Bathymetric effects on the flow are more obvious at $t = \pi/2$, when the wind is shifting to an onshore direction. In general, however, the circulation driven by cross-shelf wind stress is coherent on large horizontal scales relative to the response to alongshelf forcing.

The shelf-scale patterns reflected in the response to τ^y (Fig. 5) and τ^x (Fig. 6) at 0.438 cpd are similar to those occurring at lower frequencies. However, mesoscale variations are not nearly as apparent in the synoptic band. Secondary circulation characteristics are most significant when τ^y is weak (Fig. 5b), but otherwise the flow exhibits a strong alongshelf tendency, with an appropriate surface Ekman adjustment. As the frequency of forcing increases, the relative importance of bathymetric steering is reduced. A similar trend has been noted for model runs featuring idealized bathymetric changes (cf. Haidvogel and Brink 1986; Schwing 1989a). Again the response to cross-shelf wind forcing (Fig. 6) is spatially coherent over larger scales than is the τ^y response.

c. Comparison with observations

The cross-shelf component of wind stress during CASP was relatively small, and the observed current response to it was generally weak (Schwing 1992). Model solutions suggest that this response is relatively uniform in space and that the resulting flow is primarily alongshelf. In addition, the observed τ^x response was confined near the surface. Therefore, comparisons between depth-averaged velocity calculated from numerical model results and those determined from regression analysis of the observations are limited to the alongshelf stress response.

The model velocity field in the CASP region is compared to the observed surface and deeper flows at 0.125 cpd (Fig. 7) and 0.438 cpd (Fig. 8). Model circulation is represented by the lighter vectors. The observed near-surface (<50-m depth) velocity response is denoted by the heavy solid vectors, and the deeper response by broken vectors. Observations are representative of all instruments at a mooring, and are usually given for the meters most coherent with wind stress.

Near-surface observations display a systematic anticyclonic rotation from model results, while currents below 50 m are oriented cyclonically relative to the model. This is due in part to the fact that the model provides an estimate of the depth-averaged velocity, while observations were obtained at discrete depths. The model, of course, implicitly includes surface and bottom Ekman spirals in the parameterization of stresses, although the vertical structure of the current does not appear in the solutions. A barotropic depth-variable model of the western Scotian Shelf (Lynch et al. 1992) shows little velocity change with depth; however, flow in the bottom Ekman layer veers cyclonically. The direction of the depth-integrated transport, determined from the observed responses, is more consistent with model results.

In general, variations in the direction of flow implied by the observed velocity responses are reproduced in the model solutions. Flow at stations inside the 100-m isobath near Halifax exhibits a very strong eastward, primarily alongshelf flow. The current at the Liscomb line was predominantly offshore, as predicted by the model. The observed velocity in Emerald Basin and west of the Halifax line is also consistent with the more variable, bathymetrically controlled circulation suggested by the model in these regions. For example, the westward flow at 0.125 cpd (Fig. 7b) and onshelf flow at 0.438 cpd (Fig. 8b) at the deepest station (S4) are reproduced. The observed and model current magnitudes are also fairly comparable near the coast. However, the velocity responses at stations beyond the 100-m isobath are rather large relative to model estimates.

Observed (solid vectors) and modeled (broken vectors) alongshelf velocity and SSP responses to τ^y are compared in Fig. 9, using the Argand diagrams introduced in Schwing (1992). A consideration of the

.125cpd

a) $t=0$

b) $t=\pi/2$



FIG. 3. Model response of transport to alongshelf wind stress, at 0.125 cpd. Wind field is zero backward of Louisbourg ($0 < y < 150$ km), and 1 Pa forward of Louisbourg. Transport shown at (a) $t = 0$ and (b) $t = \pi/2$. Vector units are $\text{m}^2 \text{s}^{-1} / \text{Pa}$. White areas denote transport less than $1 \text{ m}^2 \text{s}^{-1} / \text{Pa}$.

.125cpd

a) $t=0$

b) $t=\pi/2$

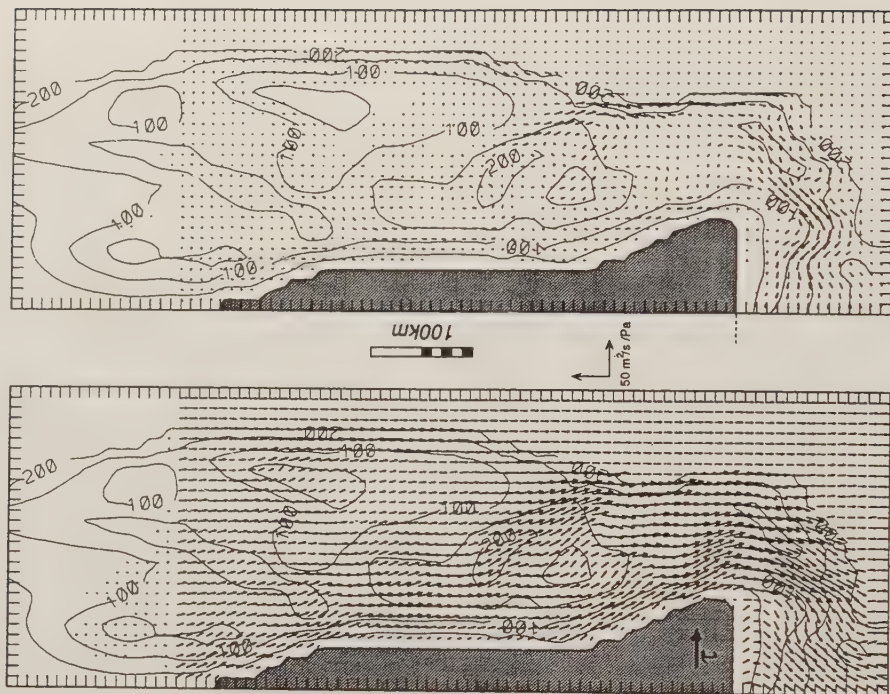


FIG. 4. Model response of transport to cross-shelf wind stress, at 0.125 cpd. Wind field is zero backward of Louisbourg and is 1 Pa forward of Louisbourg. Transport shown at (a) $t = 0$ and (b) $t = \pi/2$. Vector units are $\text{m}^2 \text{s}^{-1} / \text{Pa}$. White areas denote transport less than $1 \text{ m}^2 \text{s}^{-1} / \text{Pa}$.

.438cpd

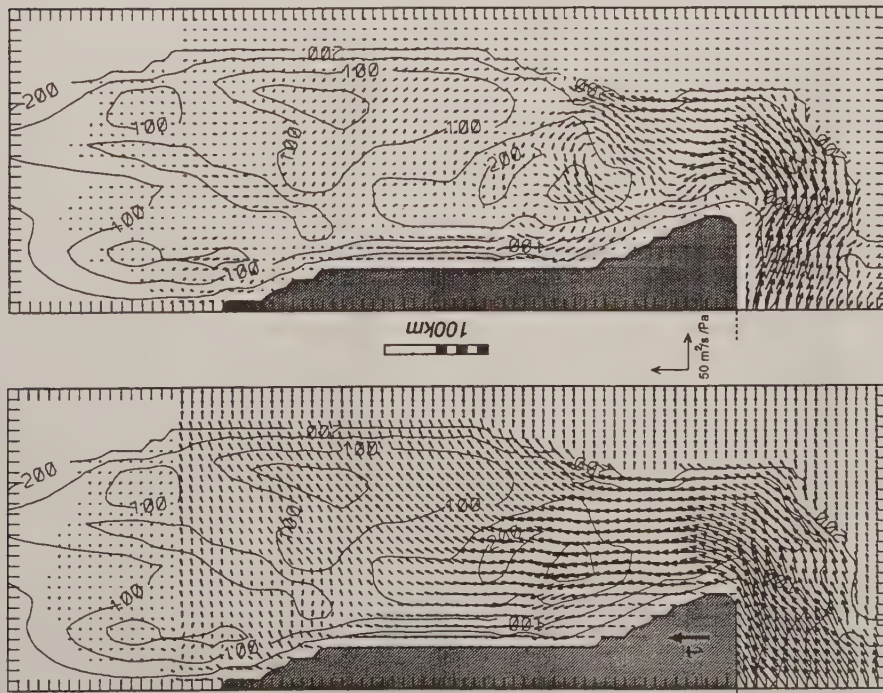
a) $t=0$ b) $t=\pi/2$ 

FIG. 5. Model response of transport to alongshelf wind stress, at 0.438 cpd. Wind field is zero backward of Louisbourg and 1 Pa forward of Louisbourg. Transport shown at (a) $t = 0$ and (b) $t = \pi/2$. Vector units are $\text{m}^2 \text{s}^{-1} / \text{Pa}$. White areas denote transport less than $1 \text{ m}^2 \text{s}^{-1} / \text{Pa}$.

.438cpd

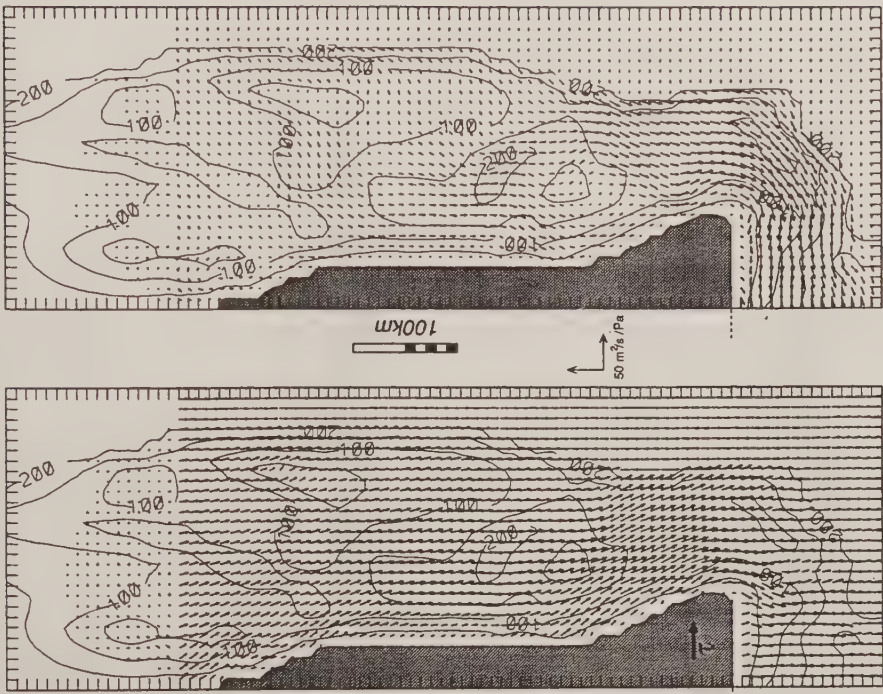
a) $t=0$ b) $t=\pi/2$ 

FIG. 6. Model response of transport to cross-shelf wind stress, at 0.438 cpd. Wind field is zero backward of Louisbourg and 1 Pa forward of Louisbourg. Transport shown at (a) $t = 0$ and (b) $t = \pi/2$. Vector units are $\text{m}^2 \text{s}^{-1} / \text{Pa}$. White areas denote transport less than $1 \text{ m}^2 \text{s}^{-1} / \text{Pa}$.

$$\omega = .125\text{cpd}$$

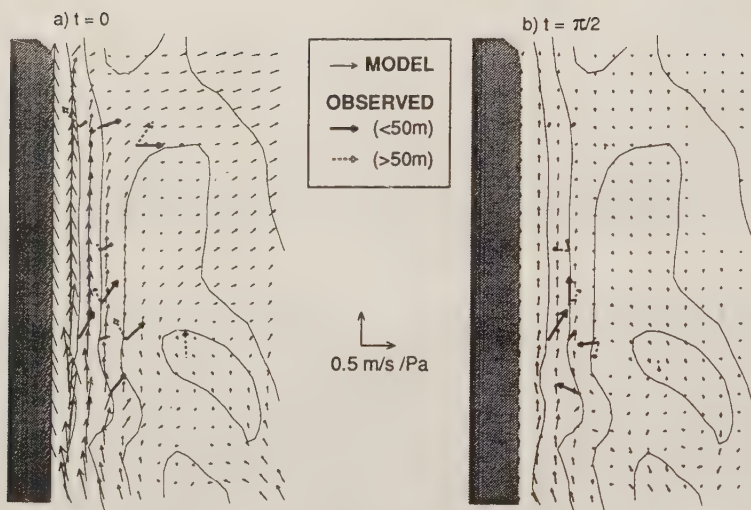


FIG. 7. Comparison of observed velocity to model results, for 1 Pa periodic alongshelf wind stress forcing at 0.125 cpd, at (a) $t = 0$ and (b) $t = \pi/2$. Results are expressed in units of $\text{m s}^{-1}/\text{Pa}$. Model velocity denoted by lighter vectors. Observed near-surface (<50 m) velocity at CASP moorings denoted by bold vectors, deeper (>50 m) velocity denoted by broken vectors. Observations based on typical transfer response determined by multiple regression analysis in Schwing (1992).

$$\omega = .438\text{cpd}$$

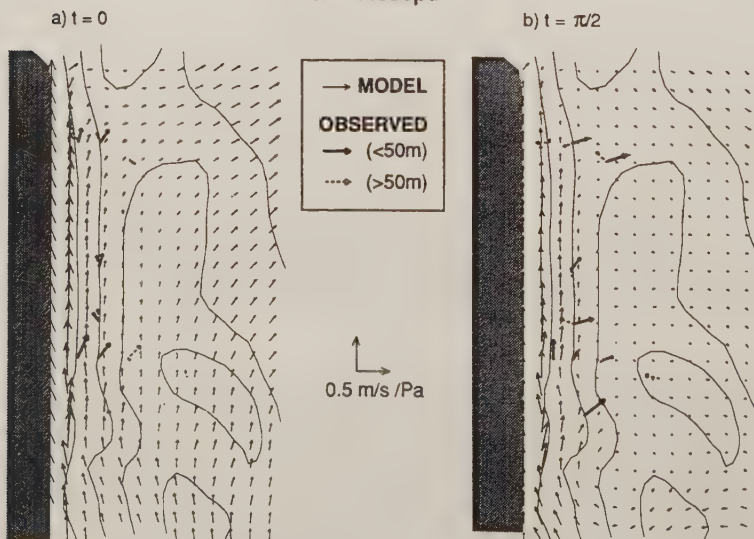


FIG. 8. Comparison of observed velocity to model results, for 1 Pa periodic alongshelf wind stress forcing at 0.438 cpd, at (a) $t = 0$ and (b) $t = \pi/2$. Results are expressed in units of $\text{m s}^{-1}/\text{Pa}$. Model velocity denoted by lighter vectors. Observed near-surface (<50 m) velocity at CASP moorings denoted by bold vectors, deeper (>50 m) velocity denoted by broken vectors. Observations based on typical transfer response determined by multiple regression analysis in Schwing (1992).

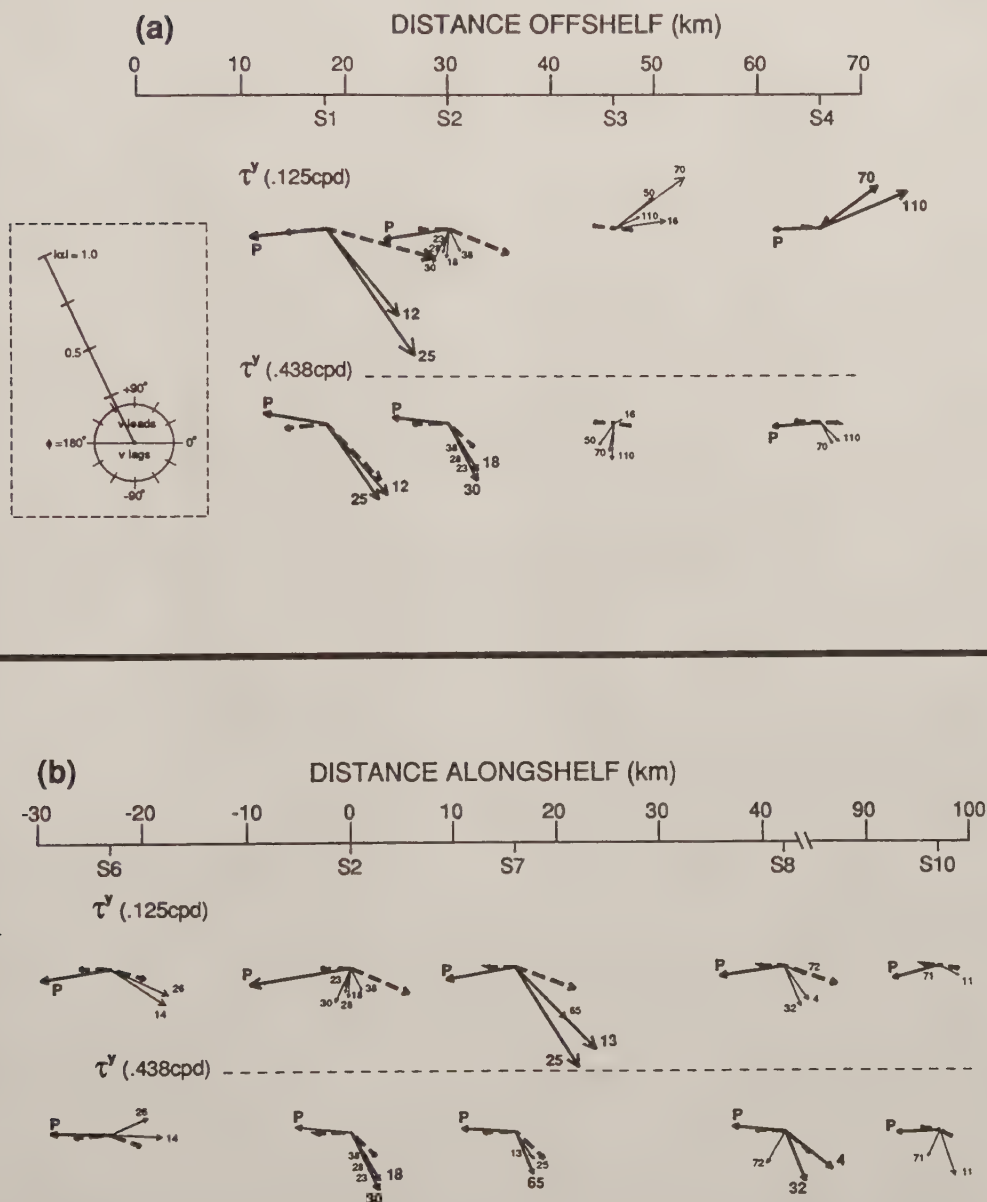


FIG. 9. Comparison of observed and model responses of v to alongshelf wind stress forcing at 0.125 and 0.438 cpd, for stations in the (a) Halifax line and (b) 100-m isobath line. Vectors describe amplitude and phase of response. Model results (broken vectors) adapted from Figs. 3 and 5. Observations (solid vectors) based on multiple regression analysis of Schwing (1992); bold vectors denote 95% significance.

alongshelf current alone shows that the model estimate of that component is somewhat better. The observed alongshelf response is fairly uniform with depth, in contrast with the cross-shelf velocity component. However, the amplitude of v at stations beyond the

100-m isobath is still underestimated by a factor of 2 or more, particularly at 0.125 cpd. The stronger flow at $t = \pi/2$ (Figs. 7b and 8b) is due in part to larger phase differences between the measured current and τ^y than the model suggests. The model typically leads

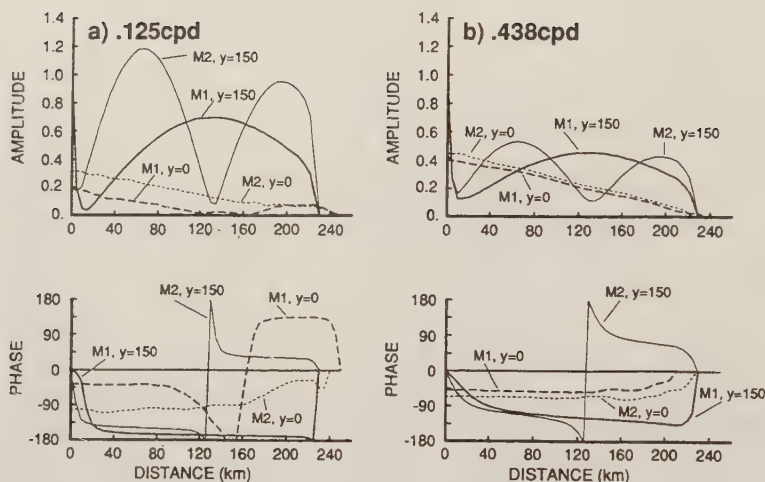


FIG. 10. Model amplitude and phase of SSP at backward cross-shelf boundary ($y = 150$ km) and transect off Louisbourg ($y = 0$) at (a) 0.125 cpd and (b) 0.438 cpd. Solutions are forced by mode 1 (M1) or mode 2 (M2) incident CTW at $y = 150$ km. Amplitude normalized by coastal SSP at origin. Phase in degrees relative to origin. Cross-shelf distance relative to coast.

observations by 10–15 h at 0.125 cpd, and 3–6 h at 0.438 cpd.

Although the model and observed SSP phases at the CASP moorings in both frequency bands agree within about 2–3 h, the observed SSP amplitude is again about twice that of the model (Fig. 9). Coastal SSP magnitudes are consistently underestimated by the model as well. If Sable Island wind underestimates stress over the CASP region, then the observed gains would be overestimated. Wind stress near the coast, where the observed and model gains are similar, is reduced (Smith 1987), so Sable Island wind may be more representative in coastal areas. However, since changes in coastal SSP are associated with the velocity response integrated across the entire shelf, then nearshore and coastal pressure would be underestimated by the model. The role of spatially inhomogeneous wind forcing is an area worth examining with future models. Theoretical work by Chapman (1987) shows that model predictions are most sensitive to the quality of wind stress forcing.

Alternatively, the bottom friction coefficient (r) may be wrong or improperly parameterized. Flow increases when the value of r is reduced (Haidvogel and Brink 1986) or varies inversely with depth (cf. Hopkins and Dieterle 1983; Chapman et al. 1986). As noted previously, however, sensitivity studies with the model used here indicate that current speed is relatively unaffected (less than 20%) by realistic changes in r . Another possibility is that the model grid smooths out details in the true bottom and coastline that may produce locally stronger currents.

4. Model results for nonlocal forcing: Coastally trapped waves?

a. Response to an incident CTW at the backward boundary

The circulation induced by a single-mode periodic CTW propagating across the backward boundary ($y = 150$ km) is described in this section. Again results are compared at $\omega = 0.125$ and 0.438 cpd. The structures of the incident mode 1 and 2 CTWs at the backward boundary are shown in Fig. 10. To be consistent with the statistical results from Schwing (1992), transport is calculated from the pressure field normalized by Louisbourg SSP ($y = 0$) and is expressed in units of $m^2 s^{-1}/m$. Transport phase is also set relative to Louisbourg SSP. Vectors in the region east of Louisbourg have been omitted for clarity.

The mode 1 contribution to Scotian Shelf circulation at 0.125 cpd (Fig. 11) is steered around shallow areas, resulting in quiescent regions over Sable Island Bank and near the coast. To compensate, transport increases through the deeper areas of the shelf. This is opposite the locally forced response (Fig. 3), where flow is stronger in shallower areas. A substantial amount of the flow is deflected offshore and against the incident transport by Sable Island Bank. Transport decreases in magnitude in the forward direction, probably because of wave scattering by irregular bathymetry and strong bottom stress over shallow regions. The SSP in the CASP region lags Louisbourg SSP by about 10° , and is approximately out of phase with local transport.

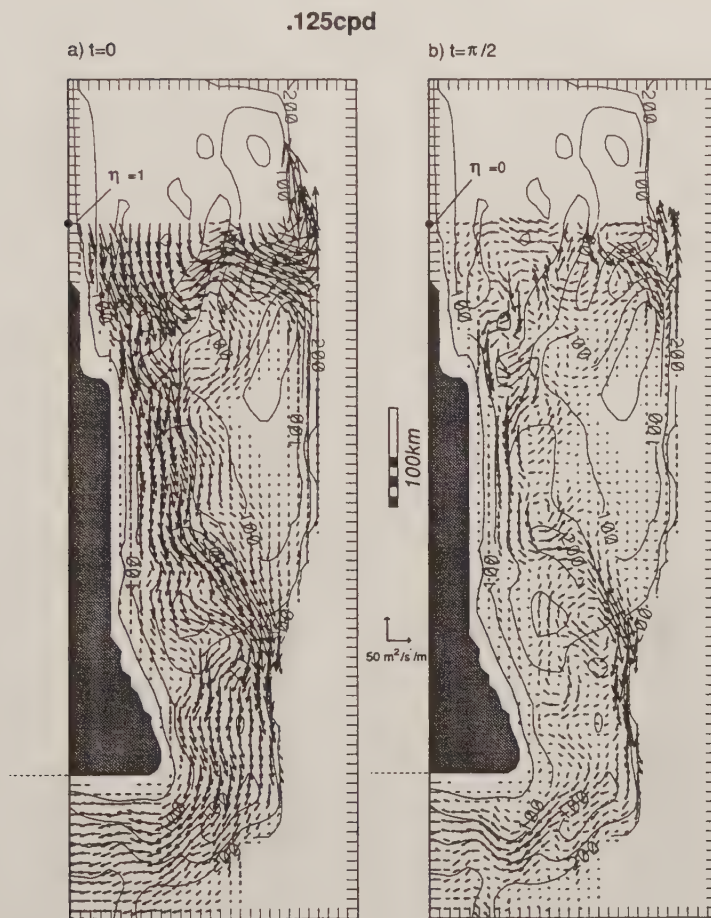


FIG. 11. Model transport, forced at backward boundary ($y = 150$ km) by mode 1 CTW periodic at 0.125 cpd, at (a) $t = 0$ and (b) $t = \pi/2$. Vector lengths are normalized by Louisbourg SSP; units are $\text{m}^2 \text{s}^{-1}/\text{Pa}$. Transport in region $0 < y < 150$ km omitted for clarity. White areas forward of origin ($y < 0$ km) denote transport less than $1 \text{ m}^2 \text{s}^{-1}/\text{Pa}$.

Thus, maximum SSP is nearly coincident with maximum transport in the forward direction, and the resulting current is in geostrophic balance with the cross-shelf gradient, as suggested by Schwing (1992). Transport at $t = \pi/2$ (Fig. 11b), when SSP at the backward boundary and over most of the shelf is falling, especially reflects the complicated flow regime seen in the wind-forced responses. The meandering circulation pattern again is linked closely to bathymetric changes.

As with the wind-forced case, the pattern and magnitude of the remotely forced flow west of Halifax display excellent agreement with the steady numerical solutions of Wright et al. (1986) and Lynch et al. (1992), forced by a coastal SSP setup at Halifax. In particular, all three models show quiescent areas near the coast, and convergence and maximum transport northwest

of Browns Bank. Current speeds are similar in the region common to these models, as well.

A rather surprising model result is that the nonlocal circulation off Nova Scotia is *independent of the incident wave form* applied at the backward boundary. The solution forced by a mode 2 CTW displays a nearly identical circulation pattern to that shown in Fig. 11. The only major difference is an increased phase lag to the mode 2 wave of about 60° . This increased lag is nearly constant over the entire domain; thus, phase differences forward of Louisbourg are essentially identical for either mode. The similarity of this response, and its possible mechanism, is demonstrated in Fig. 12, which compares the amplitude of the pressure field, normalized by Louisbourg SSP, for the mode 1 and 2 incident CTWs.

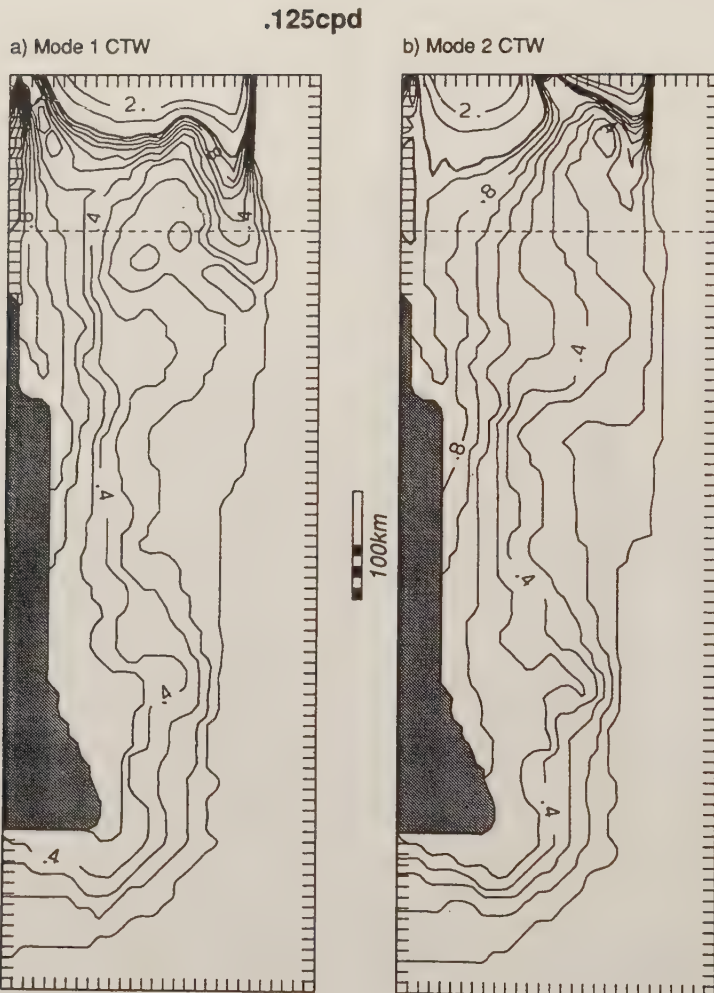


FIG. 12. Amplitude of SSP field, forced by (a) mode 1 and (b) mode 2 incident CTW at backward boundary. Amplitude normalized to Louisbourg SSP.

The highly irregular bathymetry east of Louisbourg rapidly alters the incident wave structure, resulting in a nearly identical forward-propagating form. This rapid modification is also evident in the cross-shelf modal structure off Louisbourg, particularly at higher frequencies (Fig. 10). The outer-shelf banks seem particularly effective in dissipating and/or scattering and reflecting wave energy. Modal differences in the incident wave are greatest in this region.

The nonlocal response is less restricted to deeper shelf regions at 0.438 cpd (Fig. 13). Mesoscale variations in the flow at $t = 0$ again occur in association with strong bathymetric changes. However, these small-scale features are less pronounced at higher frequencies, a relationship also seen in the idealized CTW model

results of Schwing (1989a), as well as in the local wind-forced response described in section 3. Increasing ω decreases the length of the "shadow zone" forward of a bathymetric feature (Wilkin and Chapman 1987). The magnitude of the transport at $t = \pi/2$ is relatively strong, reflecting the greater ($\sim 30^\circ$) phase lag of SSP in the CASP region of the model to Louisbourg.

b. Comparison with observations

Model and observed coastal SSP responses to remote forcing show good general agreement (Schwing 1989b). Correlation between the observed and modeled velocity responses will confirm the model's ability to reproduce this relationship on smaller spatial scales. The transfer functions between CASP alongshelf velocity and

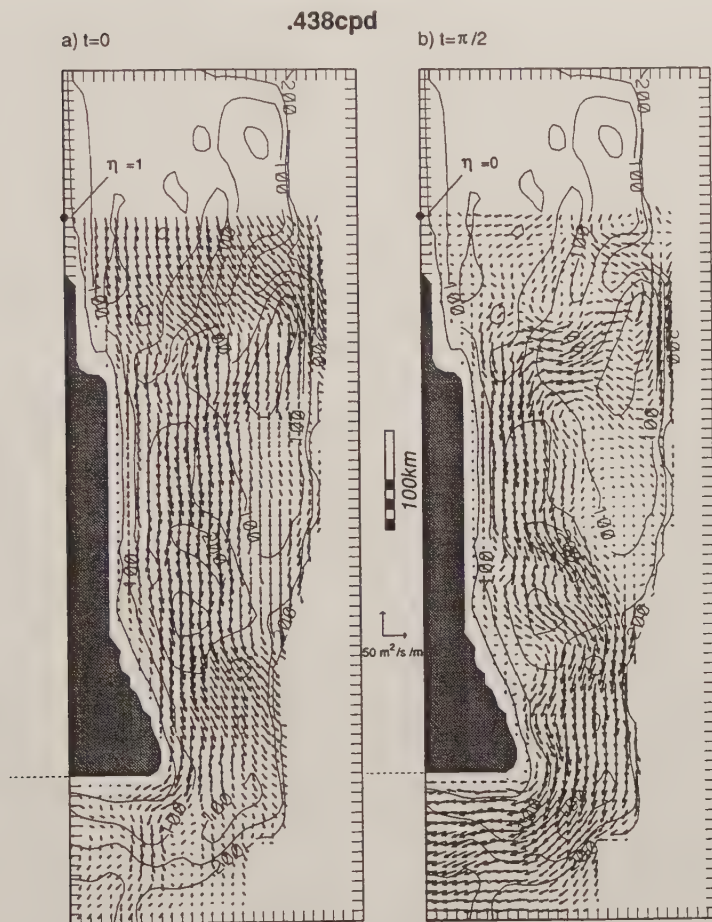


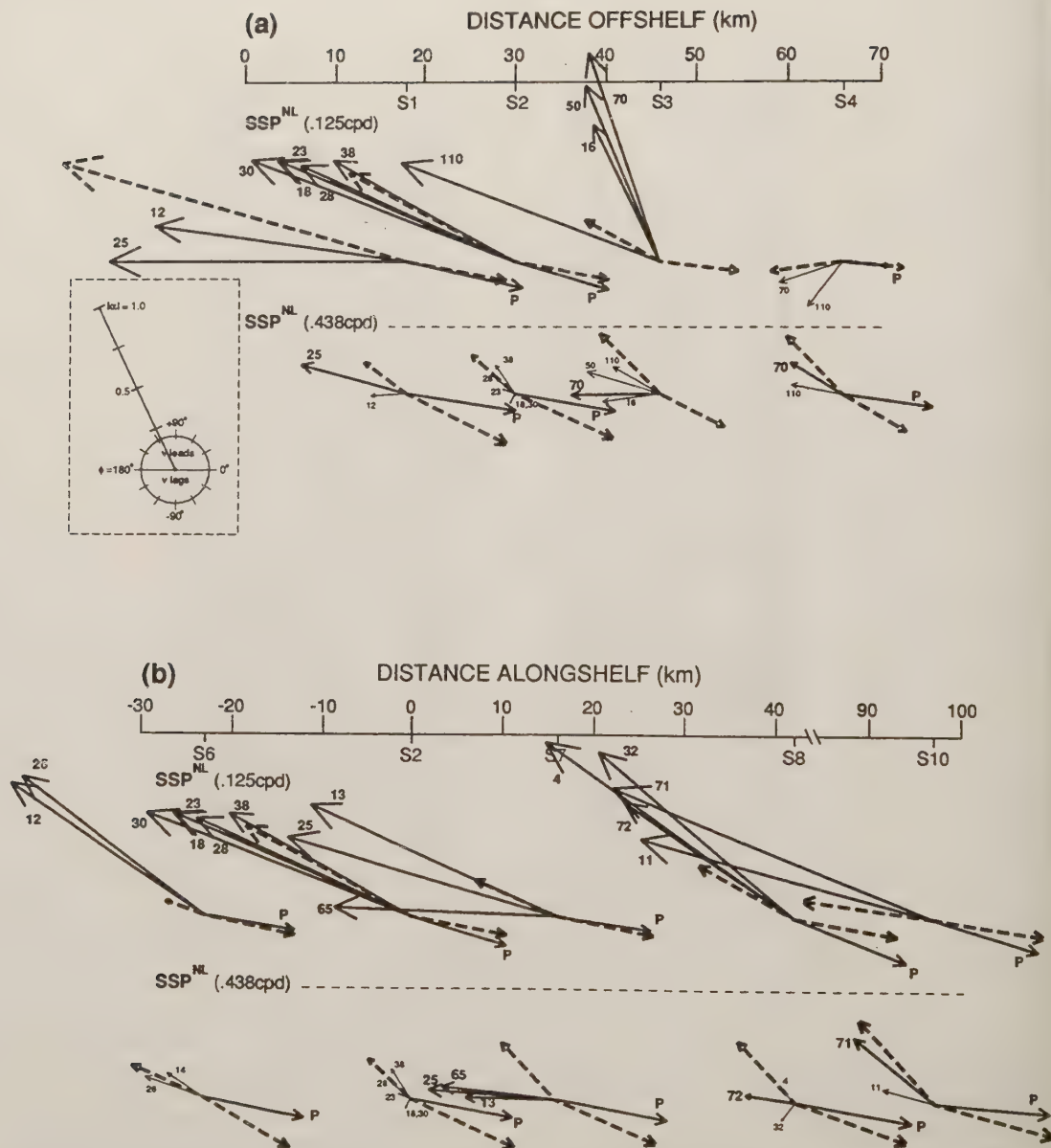
FIG. 13. Model transport, forced at backward boundary by mode 1 CTW periodic at 0.438 cpd, at (a) $t = 0$ and (b) $t = \pi/2$. Vector lengths are normalized by Louisbourg SSP; vector units are $\text{m}^2 \text{s}^{-1}/\text{Pa}$. Transport in region $0 < y < 150 \text{ km}$ omitted for clarity. White areas forward of origin denote transport less than $1 \text{ m}^2 \text{s}^{-1}/\text{Pa}$.

Louisbourg SSP at 0.125 cpd and 0.438 cpd, taken from Schwing (1992), are compared to the mode 1 CTW model results in Fig. 14.

Remotely forced observations are very comparable to model alongshelf velocity and SSP at most stations. Model results replicate observed phase differences to within about 10° in most cases, and match observed gains in the synoptic band as well. As with the wind-forced simulations, however, model velocities at the offshore stations generally underestimate observations at 0.125 cpd, despite the fact that SSP gains are quite similar. Remotely forced geostrophic flow through the Halifax line was estimated from the cross-shelf pressure gradient and the alongshelf velocity response (Schwing 1992). While these independent estimates are reasonably close at higher frequencies, this analysis suggests

that the pressure gradient is not large enough to balance the observed alongshelf flow at 0.125 cpd.

The mode 1 wave-forced solution (Fig. 11) exhibits a phase speed of $\sim 17 \text{ m s}^{-1}$ and a decay scale of $\sim 800 \text{ km}$ at 0.125 cpd, while these parameters are about 27 m s^{-1} and 1200 km at 0.438 cpd, based on coastal SSP results. Nearly identical values are obtained from the mode 2 results, validating the independence of the flow field from the incident wave structure. The observed exponential decay scale based on coastal SSP is similar (Schwing 1989b, 1992), suggesting that the parameterization of bottom friction is reasonable. The phase speed determined from observed coastal SSP is nearly identical to the model results at 0.438 cpd, but overestimated by a factor of ~ 3 at 0.125 cpd. Of course, these model characteristics vary greatly on small spatial



scales; the aforementioned values are averaged along the entire shelf.

The discrepancy between observations and the model results supports the idea that the low-frequency circulation includes a strong ageostrophic component. Another possibility is that energy scattered into higher

wave modes may add substantially to the total current but contribute little to the SSP signal, which is strongly biased toward the lowest mode (Hsieh 1982). This imbalance also holds true for the observed response to τ^y (Schwing 1992), and thus may partially account for the relatively small model currents in the vicinity of

Emerald Basin. It was also shown that flow at nearshore stations exhibits a response more typical of the integrated circulation. This may explain why model results fit observations better at the nearshore stations.

Of course, baroclinic effects, which may inhibit the scattering or dissipation of higher modes (Chapman 1983), cannot be ruled out as a potentially important source of variability beyond the 100-m isobath. Interaction between the remote response and local wind forcing that was not properly separated by the statistical models is also a possibility. Future modeling efforts of the Scotian Shelf should carefully examine these effects.

5. Discussion and summary

Statistical analysis of the CASP data has defined the important subtidal scales and patterns of the Scotian Shelf circulation (Schwing 1989a,b, 1992). A hierarchy of analytical and numerical models was also developed by Schwing (1989a) to provide a physical basis for understanding what processes may be responsible for the variability observed during CASP. Results from these idealized models indicate that bathymetric irregularities have a profound influence on flow in coastal regions. The primary goal of this paper has been to develop a numerical model of the Scotian Shelf circulation that features realistic bathymetry, whose results could be compared directly to SSP and velocity observations.

The most interesting model result is the presence of several circulation features associated with bathymetric changes. The flow displays a strong tendency to parallel f/h contours where the bathymetry is relatively smooth and bottom gradients are weak. However, closed circulation cells of order 50–100 km in diameter develop over steep bathymetry. The vorticity balance is given by taking the curl of (1)–(2) and substituting for $\nabla \cdot \mathbf{v}$ from (3):

$$\left(\xi - \frac{f}{h} \eta \right)_t - \frac{f}{h} \mathbf{v} \cdot \nabla h - \nabla \times \left(\frac{\tau - r\mathbf{v}}{h} \right) = 0, \quad (12)$$

where $\xi = v_x - u_y$ is the relative vorticity. The first term in (12) is the time rate of change of relative vorticity less the effect of changes in the free surface; the second represents local cross-isobath flow (vortex tube stretching); and the final term is the curl of the surface minus bottom stress.

The inclusion of time dependence has little effect in shallow water, as friction balances vortex stretching. The primary balance is between inertia and stretching in deep water. Over relatively flat regions, (12) is simply

$$\left(\xi - \frac{f}{h} \eta \right)_t = -\frac{r}{h} \xi$$

in the case of a spatially uniform wind, or $\epsilon \xi = 0$ with the rigid-lid approximation. The vorticity balance is between inertia and bottom stress. However, the vortex

stretching term becomes large over steep bathymetry. An area of vortex squashing, which creates negative relative vorticity, develops over a region of shoaling bathymetry. Vortex stretching and the resultant generation of positive vorticity occurs over deepening bathymetry. The circulation associated with Emerald Basin, for example, is deflected to the left (right) over the deepening (shoaling) portion of the basin, to balance the generation of positive (negative) relative vorticity. In contrast, no mechanism for generating vorticity exists where the depth is constant.

It is important to note that the bathymetric contribution to the amplitude of the pressure field is not nearly as significant as it is to the magnitude and direction of the current. For the spatial scales typical of the Scotian Shelf, the influence of bathymetry modifies the response of the pressure field by less than 10% of coastal SSP, but increases the transport by as much as a third and changes the direction of the flow on the order of 30° (Schwing 1989a). Given these results, it is not surprising that the observed current patterns on the rugged Scotian Shelf are so incoherent, while SSP is highly correlated over large horizontal separations. Despite the extremely irregular bathymetry of the Scotian Shelf, it is possible to describe the interaction between circulation and bathymetry on relatively small horizontal scales with a properly resolved numerical model and relate observed patterns to fundamental dynamical balances. However, it is obviously not possible to monitor the transient shelf circulation with coastal sea level measurements or a limited array of SSP gauges.

Numerical model results generally reproduce the diverse local and nonlocal velocity responses observed in the CASP data. The model appears most effective at explaining the circulation induced by motions propagating onto the shelf from the east. The amplitude and phase of the observed SSP and velocity responses to nonlocal forcing are nearly identical at most stations (Fig. 14). The exponential decay scales estimated from model and observed SSP are consistent, although the model phase speed differs from that determined from the observations. More significantly, the circulation forward of Louisbourg is *independent* of the incident wave structure at the backward boundary, only 150 km to the east, suggesting that bathymetry rapidly modifies the propagating free signal. Given the extremely rugged shelf bathymetry and the apparently strong influence of bottom stress, it is believed that the incident wave is continuously scattered into higher modes (Wilkin and Chapman 1990) that are dissipated over small horizontal scales (Webster 1985).

The reproduction of the observed variations forced by wind stress over the Scotian Shelf is less successful, although the general circulation patterns within the CASP array are seen in the model results. Discrepancies in the amplitude of the observed and model responses to local wind forcing are noted over the deeper portions

of the shelf, which may be due to mesoscale variability in the wind field. Much of the perceived variability in the direction of flow is due to the depth-integrated aspect of model transport. However, variations in u are difficult to quantify. The ability to adequately describe the cross-shelf flow remains one of the outstanding problems in coastal oceanography.

Some of the discrepancy between the offshore CASP and model circulation, in both local and nonlocal responses, may be associated with baroclinic effects. Baroclinicity undoubtedly influences Scotian Shelf circulation, particularly over the outer portion of the shelf (Petrie 1983). There is, however, some justification for a barotropic model. First, the structure of the shelf water in winter within most of the CASP array and over much of the shelf is well mixed to the bottom (Smith et al. 1978; Schwing 1992). The alongshelf current response during CASP generally does not display the significant depth variability that would be expected in the case of baroclinic flow (Schwing 1992). Anderson and Smith (1989) conclude that the mean circulation is predominantly barotropic. The importance of baroclinic motions is probably limited to near-inertial (Smith 1989) or seasonal time scales. Major variations in the pycnocline position during CASP occurred at periods longer than 10 d, particularly in the near-surface layer and the inner portion of the shelf (Lively 1988). Thus, the baroclinic contribution to the synoptic frequency (barotropic) fluctuations of interest in this study is probably limited to a relatively steady background flow (i.e., the Nova Scotian Current).

Finally, the qualified success with which the model replicates the observed locally and, particularly, remotely generated flow patterns in the shelf region covered by the CASP array implies that much of the circulation may be barotropic. Previous barotropic numerical studies in this region have been instructive (cf. Beardsley and Haidvogel 1981; Wright et al. 1986). However, the potential importance of baroclinicity on the outer shelf must be considered. A natural extension to this work is the application of a stratified model to the Scotian Shelf region.

Perhaps more important, the statistical model results obtained by Schwing (1992) for offshore stations (i.e., S3, S4, S11) generally have large confidence intervals. Thus, the observed responses shown in Figs. 7–9 only approximate the highly variable wind-forced response on the mid- and outer shelf. It may not be possible to say with certainty what contributes to the large flows in deeper water, or even if such fluctuations are caused by meteorological forcing directly over the Scotian Shelf. Given the limited spatial extent of the CASP array, it is impossible to validate the barotropic model results over the outer shelf. In addition, substantial differences in the flow at the resolution of the model mesh mean that imprecise placement of mooring positions within the model domain could lead to some of the poor agreement. Nevertheless, the general compati-

bility between the observed and model responses to wind forcing gives some credence to the idea that complex shelf circulation features periodic at subtidal frequencies are closely coupled to mesoscale bathymetric variations.

In light of previous theoretical investigations on the effect of idealized and realistic bottom features on circulation, these results are not surprising. The majority of previous studies concerning bathymetric influences have dealt primarily with bathymetric effects on CTWs (Wang 1980; Brink 1986; Wilkin and Chapman 1987, 1990; Middleton and Wright 1988) or some form of remote forcing at the backward boundary (Greenberg and Petrie 1988), although some modeling efforts have examined modifications to the locally forced circulation (cf. Simons 1983; Haidvogel and Brink 1986; Lopez and Clarke 1988).

An early, simple linear barotropic model for the Gulf of Maine (Csanady 1974) showed that closed wind-driven barotropic circulation cells develop over idealized depth gradients, due to the generation of vorticity by stretching. Subsequently, more elaborate and bathymetrically realistic models have been used to study flow–bathymetry interaction (Beardsley and Haidvogel 1981; Wright et al. 1986; Greenberg and Petrie 1988; Lynch et al. 1992). As mentioned previously, the steady solutions of Wright et al. (1986) and Lynch et al. (1992) exhibit the same circulation patterns and scales of variability, and quantitatively agree with the results presented here. While results from a barotropic model of the Newfoundland shelf (Greenberg and Petrie 1988) do not include the closed circulation features seen on the Scotian Shelf, they do exhibit several areas of nonisobathic flow and substantial horizontal shear on the region's small bathymetric scales.

In the Middle Atlantic Bight, forward of the Scotian Shelf, realistic numerical solutions exhibit a generally alongshelf wind-driven flow that increases in amplitude to the south (Beardsley and Haidvogel 1981), and is embedded with numerous small-scale features that are tied to bathymetric variations (Hsueh 1980; Beardsley and Haidvogel 1981; Hopkins and Dieterle 1983). The moving storm experiments of Beardsley and Haidvogel, analogous to the periodic wind-forced solutions described here, also display small-scale and highly transient oscillations and a southward phase propagation. Another general conclusion is that the influence of alongshelf wind stress forcing is much greater than the cross-shelf component.

The inability to replicate the observed velocity is also not unique to this model. Brink et al. (1987) and Chapman (1987) also underestimate actual current speeds. Greenberg and Petrie's (1988) barotropic model underpredicts flow in some areas as well. The reason why many models give systematically low current speeds is not understood and may vary with the physics inherent in each study.

A novel aspect of the numerical model applied here is the separation of solutions into local and remote contributions, using two different forcing fields and backward cross-shelf boundary conditions. The uniquely complex bathymetry is a feature of only select realistic models of the region (Beardsley and Haidvogel 1981; Wright et al. 1986; Lynch et al. 1992), and unmatched by idealized models that often consider simple isolated bathymetric features. The Scotian Shelf proper has not previously been modeled with real bathymetry. The relaxation of the rigid lid allows for the inclusion of the Kelvin wave in solutions, which is shown by Lopez and Clarke (1989) to be an important contributor to the SSP field. Finally, wavelike solutions, which were sought in many earlier models, are not considered here.

Webster (1985) argues that the nonlocal response at a location is due to constructive and destructive interference of CTWs generated over the backward section of the shelf. The number and structure of wave modes contributing to the remote flow is a function of the degree of scattering and reflection of each mode and the importance of bottom stress, which determine the wavelength, frequency, mode number, and decay scale of the waves involved. It appears that higher and short wave modes are selectively dissipated over short length scales, leaving a large-scale flow that is predominated by low-mode, frictionally decaying long waves.

While the general circulation is dominated by low modes, particularly near the coast (Webster 1985), higher-mode and reflected waves may be extremely important in the vicinity of irregular bathymetric features, and may lead to the spatially incoherent flow observed during CASP. This is especially true for velocity as it reflects the structure of the free response more accurately than SSP, which is strongly biased for the lowest mode (Hsieh 1982). The strength and phase of the current varies substantially over short spatial scales in scattering regions (Wilkin and Chapman 1990). For highly idealized bathymetry (i.e., a single feature), solutions can be treated with relatively few wave modes. But the bathymetric length scales on the Scotian Shelf are too short to allow for a reasonable description of the circulation with wavelike solutions. Thus, a modal approach can be very inefficient at representing realistic flows over complex bathymetry.

The similar patterns induced by the mode 1 and 2 incident waves in Figs. 11–13, and similarities between the wind-forced and free solutions, further focus on the ambiguity of wavelike solutions (Brink 1986). A more logical approach is to consider the total circulation to be composed of local and remote influences, as suggested by Gill and Schumann (1974) and others. Lopez and Clarke (1989) show that, without the local response, too many wave modes are required to accurately describe the low-frequency velocity field. The local contribution can be described by a diffusive-like solution analogous to the ATW solution first presented

by Csanady (1978), while the remotely generated portion is possibly defined by the familiar modal forms of the CTW theory. However, both contributions are greatly influenced by the local bathymetry, as well as by the bottom structure over which the flow has propagated.

The separation of the “local” and “nonlocal” contributions is an arbitrary one, dependent upon the position of the backward boundary. This is because pressure or current at any location is a continuum of propagating signals, each generated by wind forcing somewhere backward from that point, and continually modified by additional variations in surface and bottom stress and bathymetry. The striking coherence between the circulation driven by direct wind stress forcing over the region of interest (Figs. 2–8) and CTWs propagating from a distant source (Figs. 11–13) dramatically demonstrates this. It also further strengthens the argument for dynamical models that combine local and remote effects, rather than seek modal solutions or consider only local wind forcing. The key to the success of this approach is properly selecting a physically reasonable position for the backward boundary (e.g., the eastern edge of the shelf).

While this study has highlighted the importance of local and remote forcing and the interaction between flow and bathymetry, it also has set the stage for further investigations. Although observed and modeled results suggest that baroclinic and nonlinear motions during CASP are minor (Schwing 1989a), such effects should be considered in future models. Variability in the flow due to, and on the scales of, spatial inhomogeneities in the wind field have not been considered here. Smith (1989) stresses the need to define the mesoscale wind field to model inertial waves accurately. The numerical model developed here can be modified easily to examine the role of wind curl in subtidal motions as well.

Finally, while the significance of remotely generated motions has been demonstrated, their source is unknown. Is there an energy flux across the Laurentian Channel, or out of the Gulf of St. Lawrence? The model results presented here, which demonstrate that bathymetric steering is very strong, imply a gulf origin. Recent theoretical work by Middleton (1991) suggests that, for the dimensions of the Cabot Strait, a Kelvin wave propagating out of the gulf is the primary source of these motions. Only about 20% of the energy may be due to waves crossing the Laurentian Channel. Wang (1980) has shown that a cross-shelf canyon is an effective energy sink to free waves. However, an incident wave that is long relative to the canyon width should pass over that feature relatively easily (Wang 1980; Middleton and Wright 1988). Obviously, more work is required to verify the source of remote energy.

Results from the CASP meteorological experiment, and an existing knowledge of the typical storm track (Lewis and Moran 1984), have improved the capability for predicting the Scotian Shelf mesoscale wind field.

This will hopefully lead to better estimates of the wind-driven shelf flow. Once the origin of nonlocal energy is known, free motions will become easier to forecast as well. Given the qualitative success of the local and remote models, this raises the intriguing possibility of developing predictive models to detail the subtidal circulation of the Scotian Shelf and other coastal regions. In the interim, it is hoped that the results presented here provide a useful guide for establishing the proper backward boundary condition for Gulf of Maine–Middle Atlantic Bight models, and will serve as a reference point for further model development as well as a base for planning future observational studies on the Scotian Shelf.

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APPENDIX A

Finite-Difference Solutions for the Numerical Model

The discretized model domain consists of $(I + 1) \times (J + 1)$ mesh points in the x (cross-shelf) and y (alongshelf) dimensions, respectively (Fig. A1). The continuous variables in x and y are replaced by discrete variables at points i, j , defined by

$$x = i\Delta x \quad i = 0, 1, \dots, I, \quad (\text{A1a})$$

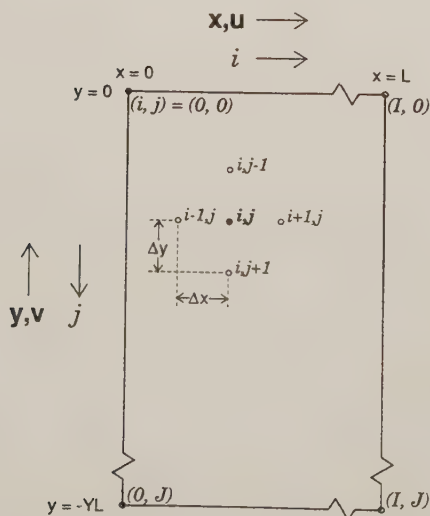


FIG. A1. Schematic showing coordinate system and model domain used in numerical model.

$$y = -j\Delta y \quad j = 0, 1, \dots, J, \quad (\text{A1b})$$

where Δx and Δy are the finite-difference intervals in the x and y directions, respectively.

The centered space finite-difference form of (7) is

$$\begin{aligned} p_{i,j}\eta_{i,j} + q_{i,j} \left[\frac{\eta_{i+1,j} - 2\eta_{i,j} + \eta_{i-1,j}}{(\Delta x)^2} \right] \\ + r_{i,j} \left[\frac{\eta_{i+1,j} - \eta_{i-1,j}}{2\Delta x} \right] + s_{i,j} \left[\frac{\eta_{i,j-1} - 2\eta_{i,j} + \eta_{i,j+1}}{(\Delta y)^2} \right] \\ + t_{i,j} \left[\frac{\eta_{i,j-1} - \eta_{i,j+1}}{2\Delta y} \right] \\ + 0((\Delta x)^2 + (\Delta y)^2) = F_{i,j}, \quad (\text{A2}) \end{aligned}$$

where

$$p = -\sqrt{-1} \frac{\omega}{f}$$

$$q = \frac{a^2 \epsilon}{1 + \epsilon^2}$$

$$r = \left(\frac{a^2 \epsilon}{1 + \epsilon^2} \right)_x - \left(\frac{a^2}{1 + \epsilon^2} \right)_y$$

$$s = \frac{a^2 \epsilon}{1 + \epsilon^2}$$

$$t = \left(\frac{a^2}{1 + \epsilon^2} \right)_x + \left(\frac{a^2 \epsilon}{1 + \epsilon^2} \right)_y$$

$$F = \frac{1}{f^2} \left[\left(\frac{\tau^y + \epsilon \tau^x}{1 + \epsilon^2} \right)_x + \left(\frac{\epsilon \tau^y - \tau^x}{1 + \epsilon^2} \right)_y \right].$$

Finite differences are of second-order accuracy, so the total discretization error is $O[(\Delta x)^2 + (\Delta y)^2]$.

Rearranging (A2) in terms of $\eta_{i,j}$, etc., and multiplying through by $(\Delta x)^2$, gives the general equation

$$\begin{aligned} a_{i,j}\eta_{i+1,j} + b_{i,j}\eta_{i-1,j} + c_{i,j}\eta_{i,j-1} \\ + d_{i,j}\eta_{i,j+1} + e_{i,j}\eta_{i,j} = f_{i,j}, \quad (\text{A3}) \end{aligned}$$

where

$$a_{i,j} = q_{i,j} + \frac{\Delta x}{2} r_{i,j} \quad (\text{A4a})$$

$$b_{i,j} = q_{i,j} - \frac{\Delta x}{2} r_{i,j} \quad (\text{A4b})$$

$$c_{i,j} = \delta^2 s_{i,j} + \delta \frac{\Delta x}{2} t_{i,j} \quad (\text{A4c})$$

$$d_{i,j} = \delta^2 s_{i,j} - \delta \frac{\Delta x}{2} t_{i,j} \quad (\text{A4d})$$

$$e_{i,j} = (\Delta x)^2 p_{i,j} - 2q_{i,j} - 2\delta^2 s_{i,j} \quad (\text{A4e})$$

$$f_{i,j} = (\Delta x)^2 F_{i,j}, \quad (\text{A4f})$$

and $\delta = \Delta x / \Delta y$, the ratio of mesh spacing. Equation (A3) is a linear system of equations that includes all values of $i = 0, 1, \dots, I$ and $j = 0, 1, \dots, J$, given by (A1); it can also be written in matrix notation as $A\eta = F$.

Writing (A3) in a fashion consistent with the SOR method (Young 1971, p. 73ff; Press et al. 1986, pp. 652–659) gives

$$\eta_{i,j}^{*n} = [f_{i,j} - a_{i,j}\eta_{i+1,j}^n - b_{i,j}\eta_{i-1,j}^n - c_{i,j}\eta_{i,j-1}^n - d_{i,j}\eta_{i,j+1}^n] / e_{i,j},$$

where $\eta_{i,j}^{*n}$ is an estimate of $\eta_{i,j}$ obtained at each mesh point during the n th iteration. The updated value of $\eta_{i,j}$ after the n th iteration is the weighted average

$$\eta_{i,j}^n = \alpha \eta_{i,j}^{*n} + (1 - \alpha) \eta_{i,j}^{n-1}, \quad (\text{A5})$$

where $\eta_{i,j}^{n-1}$ is the value of $\eta_{i,j}$ following the previous iteration and α is the relaxation parameter. From (A5), it is apparent the solution has converged when $\eta_{i,j}^{*n} = \eta_{i,j}^{n-1}$; solutions are assumed to have converged when the norm of the differences between the old and updated values reaches some small value. For the model applied here, this is given by

$$\sum_{i=0}^I \sum_{j=0}^J |(\eta_{i,j}^{*n} - \eta_{i,j}^{n-1})| \leq 10^{-5}.$$

The key to the efficiency of SOR is optimizing α . Young (1971) provides detailed descriptions of algorithms that locate an optimal α , based on a knowledge or estimate of the spectral radius ρ . One such method, used in this work, is Chebyshev acceleration (Press et al. 1986, p. 658):

$$\begin{aligned} \alpha &= 1, & n &= 1 \\ \alpha &= \left(1 - \frac{\rho^2}{2}\right)^{-1}, & n &= 2 \\ \alpha &= \left(1 - \frac{\alpha \rho^2}{4}\right)^{-1}, & n &> 2 \\ \alpha &\rightarrow \alpha_{\text{optimal}}, & n &\rightarrow \infty. \end{aligned}$$

Initially setting $\alpha = 1$, α is adjusted after each iteration until the optimum asymptotic relaxation parameter is reached. This acts to improve the average rate of convergence, since the norm of the error always decreases with each iteration. Young (1971) relates methods for estimating ρ .

APPENDIX B

Analytical Solutions for Frictional CTWs at the Backward Boundary

To obtain analytical solutions for a single-mode CTW forcing the remote models through the backward

cross-shelf boundary (section 4), three modifications are made. First, the bathymetry at $y = 150$ km is of the exponential form $h(x) = h_1 \exp[2b(x - L_1)]$ from the coast to the shelf break ($x = L_1$), and constant ($h = h_1$) seaward to the outer alongshelf boundary. A constant Rayleigh damping coefficient $\lambda = r/h_0$ is applied to the equations of motion (1)–(2). Finally, the rigid-lid approximation is made in the continuity equation (3) so that a transport streamfunction ψ can be defined, where $\psi_x = v$ and $\psi_y = -u$. These modifications allow the vorticity equation

$$-i\epsilon \left[\left(\frac{\psi_x}{h} \right)_x + \left(\frac{\psi_y}{h} \right)_y \right] = \left(\frac{\psi_y}{h} \right)_x - \left(\frac{\psi_x}{h} \right)_y \quad (\text{B1})$$

to be derived from (1)–(3). The Rayleigh form of friction in (B1) means that

$$\epsilon = \left(i \frac{\dot{\omega}}{f} + \frac{\lambda}{f} \right)$$

is a constant.

Solutions to (B1) are assumed to be of the separable, periodic form

$$\psi = \phi(x) \exp[i(\omega t - ly)], \quad (\text{B2})$$

where ω is the frequency and $l^\pm = l_{\bar{r}}^\pm \pm i l_{\bar{g}}^\pm$ is the complex wavenumber. Exponential bathymetry, Rayleigh damping, and the rigid-lid approximation allow (B1) to be solved as a second-order ordinary differential equation with constant coefficients, expressed as

$$\phi'' - 2b\phi' - (2ibl\epsilon^{-1} + l^2)\phi = 0. \quad (\text{B3})$$

The inviscid limit of (B3) reduces to an equation commonly used to determine the cross-shelf modal structure of frictionless shelf waves (cf. Wilkin and Chapman 1987; Middleton and Wright 1988).

The inclusion of a wall at the coastal and outer shelf boundaries requires

$$\psi = 0 \quad x = 0, L,$$

which allows solutions to (B3) to be simplified to the form

$$\phi = e^{bx} \sin(mx), \quad (\text{B4})$$

where $m = n\pi$ for the n th wave mode. Thus, the cross-shelf amplitude of the wave is solely a function of the mode number and bathymetric scale, and is independent of frequency and wavenumber. Dispersion curves and solutions for these conditions are very similar to those for the case of a finite-depth ocean replacing the offshore wall condition (Wilkin and Chapman 1987).

Equations (B3)–(B4) give the dispersion relation for this problem:

$$b^2 + l^2 + m^2 + 2ibl\epsilon^{-1} = 0. \quad (\text{B5})$$

Given b , m , and ϵ , it is possible to solve for the roots of l from (B5):

$$l^\pm = -b\epsilon^{-1} [1 \pm (1 - \epsilon^2(1 + m^2/b^2))^{1/2}],$$

where l^+ propagates energy in the $+y$ direction (the short wave) and l^- in the $-y$ direction (the long wave). The wavelength of l is $2\pi/l_R^{-1}$ and its exponential decay scale is $|l_T^{-1}|$, with the sign of l_T^{-1} denoting the direction in which the wave decays.

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Leatherback turtle captured by ingestion of squid bait on swordfish longline

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The leatherback turtle *Dermochelys coriacea* is the only species of the family Dermochelyidae. The other six extant marine turtles are hard-shelled members of the family Cheloniidae. The leatherback inhabits the pelagic marine environment, apparently only leaving to breed in coastal waters. With recorded dives to 475m, it is among the world's deepest-diving vertebrates (Eckert et al. 1986). With weights up to 916 kg, it is the world's largest turtle (Eckert and Luginbuhl 1988). The leatherback is listed as endangered under the U.S. Endangered Species Act, the International Union for Conservation of Nature, and the Convention on International Trade in Endangered Species. Consequently, fishery interactions involving the leatherback are of concern. This paper reports an interaction with longline gear while fishing for swordfish.

Leatherbacks ingest and become entangled in marine debris (Balazs 1985), and they are taken by operative fishing gear (Nishemura and Nakahigashi 1990). Entanglement has been reported with lobster pot lines (Lazell 1976), drift nets (Balazs 1982, Wetherall et al. In Press); pelagic longline (Witzell 1984, Tobias 1991); gillnets (Margaritoulis 1986); and swordfish *Xiphias gladius* tangle nets (Frazier and Brito Montero 1990). Interactions with tuna and swordfish longline fishing have involved entanglement and foul-hooking, particularly with the leatherback's long flippers

(Honolulu Star-Bulletin 1935, Witzell 1984, Dollar 1991, Tobias 1991, USFWS 1969). In the Hawaii swordfish fishery, sightings of leatherbacks and reported interactions are not rare, particularly in the area of the seamounts above the Northwestern Hawaiian Islands (Robert Dollar, NMFS Honolulu Lab., pers. commun.). It is not uncommon for leatherbacks to become entangled in driftnets set north of Hawaii between 30° and 45°N. However, virtually nothing is known about their overall distribution, abundance, and life history including stock structure (Wetherall et al., In press). The nearest colonies of nesting leatherbacks occur in the eastern Pacific along the coast of Mexico and Costa Rica and in the western Pacific in peninsular Malaysia. To our knowledge, ingestion of baited hooks has not been reported in the literature.

Leatherbacks are known to feed on gelatinous, pelagic animals. These include the medusa of sychozoan coelenterates (true jellyfish) (Bleakney 1965, Brongersma 1969) and hydrozoan coelenterates (Portuguese man-of-war *Physalia physalis*) (Bacon 1970). Davenport (1988) and Davenport and Balazs (1991) have suggested the potential importance of bioluminescence in the predation of free-swimming colonial tunicates (pyrosomas) by leatherbacks during the night or on deep dives. Neither fish (tuna bait) nor squid (swordfish bait) have been cited in the literature as prey of

leatherbacks. Accordingly, Witzell (1984) stated that leatherbacks are not likely to be taken on a baited hook.

The present paper presents documentation of a leatherback captured after ingesting squid bait on swordfish longline gear. The chemical light sticks used to attract swordfish may have attracted the leatherback to the gear.

On 24–25 January 1991, while experimental longline fishing operations were being conducted for swordfish from the NOAA research ship *Townsend Cromwell*, a leatherback turtle was hooked and released alive at lat. 26°58.3'N, long. 168°53.5'W. The turtle swam vigorously while being hauled next to the research vessel and after being released. The hook line could be seen coming from the turtle's mouth, but the exact location of the hook was not apparent. No blood or external injuries were apparent. A tree branch lopper on the end of an extendable fiberglass pole was used to cut the hook line a few centimeters from the turtle's mouth. The estimated carapace length of the turtle was 170 cm. The turtle was too large to haul on board, and the prevalence of sharks, including blue shark *Prionace glauca*, made it impossible to enter the water for accurate measurement or tagging. Other site specifics included the following: 2400m bottom depth, 21.4°C sea surface-water temperature, 18.9°C air temperature, 150–180 cm sea swells, northeasterly trade winds at 15 kn, and approximate depth of the upper mixed layer at 85 m.

Details of the set and gear are as follows. The longline gear consisted of ~16 km of 4.0 or 3.2 mm monofilament main line suspended with floats every 3 hook lines. The gear, with 206 hooks, was set on 24

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January 1991 starting at lat. 27°01.720'N, long. 168°56.153'W, in the vicinity of an unnamed seamount some 940km east of Midway Is. and 150km north-northeast of Raita Bank, Northwestern Hawaiian Is. The gear was hauled on 25 January beginning at lat. 26°59.094'N, long. 168°57.810'W. The turtle was taken on the first hook of a 3-hook basket located about mid-set. This hook was set at 1818h and hauled at 0907h the next day, for a soak time of 14h 49 min. Because the hook timer (a 7.5×3 cm cylinder of clear plastic resin with an embedded clock chip; Somerton et al. 1988) on that line was lost, an estimate of the time of hooking is not available. The hook timer on the second hook-line, with full bait remaining, was set off at 0511h; the hook timer on the first hook of the previous basket, with the bait missing, was set off at 0159h. The float lines, made of polypropylene rope, were 9m long. The hook droppers, made of 2.1mm monofilament, were 13m long with a 60g weighted swivel 4m from the hook. Thus, the depth of hook 1 was nominally ~22m, unless altered by currents, since the first hook-line of each basket was attached within 3m of the float. Green, 12h chemical light sticks were placed ~2m above each of the 206 hooks (the light sticks still glowed weakly at the time of hauling). Each hook was baited with a whole, previously-frozen Argentinian squid (*Illex* sp.), weighing ~0.34kg.

While entanglement of leatherbacks in pelagic longline and other gears has been described, ours is apparently the first report of a hook and bait being eaten. Chemical light sticks used on swordfish longline may impose an added hazard for leatherbacks by simulating natural prey. The magnitude of the take, the level of mortality or serious injury, and the impact on the leatherback stock are unknown. Additional data on the take by pelagic fisheries as well as information on leatherback feeding habits, stock structure, and population dynamics would be needed to evaluate the impact of the take.

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Regional Differences in Otolith Morphology of the Deep Slope Red Snapper *Etelis carbunculus*

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Smith, M. K. 1992. Regional differences in otolith morphology of the deep slope red snapper *Etelis carbunculus*. Can. J. Fish. Aquat. Sci. 49: 795–804.

Sagittal otoliths from four populations of the Pacific deep slope red snapper *Etelis carbunculus* Cuvier were compared using Fourier descriptors and other shape indices, linear proportions, and dry weight. Otoliths from Hawaii, Vanuatu, Fiji and French Polynesia and a small number from the Commonwealth of the Northern Marianas Islands (NMI) were examined. Regional shape and weight characteristics were distinguishable, despite the wide range of individual variation and limited available size range from some regions. Size-specific differences in otolith shape were found for the four regions for which a sufficient sample was available. Otoliths from Hawaii, French Polynesia, and NMI showed a significant shape affinity. Otoliths from Fiji and Vanuatu were similarly shaped and were distinct from those from the other three regions. Interregional otolith shape affinities for the stocks examined parallel similarities in maximum size and growth rate from the literature, suggesting that growth rate may influence otolith shape. Observed trends in otolith weight as a function of fish length support growth-related regional differences in otolith shape.

Des otolithes sagittaux de quatre populations de vivanneaux du Pacifique (*Etelis carbunculus* Cuvier) ont été comparés à l'aide de descripteurs de Fourier et d'autres indices de taille, des proportions linéaires et du poids sec. Des otolithes provenant d'Hawaï, du Vanuatu, des Fidji et de la Polynésie française et un petit nombre du Commonwealth des îles Mariannes du Nord (IMN) ont été examinés. On pouvait distinguer des caractéristiques régionales de forme et de poids, en dépit de la grande diversité de variations individuelles et de la plage limitée des tailles disponibles pour certaines régions. On a observé les différences propres à l'espèce dans la forme des otolithes dans quatre régions pour lesquelles un échantillon suffisant était disponible. Les otolithes d'Hawaï, de la Polynésie française et des IMN présentaient une affinité de forme significative, alors que les otolithes des Fidji et de Vanuatu avaient des formes semblables et étaient distinctes de celles des trois autres régions. Les profils des affinités interrégionales des formes d'otolithes des stocks examinés sont semblables aux ressemblances des tailles maximum et des taux de croissance mentionnées dans la documentation, ce qui suggère que le taux de croissance peut influencer la forme des otolithes. Les tendances observées du poids des otolithes en fonction de la longueur du poisson appuient l'hypothèse des différences régionales en rapport avec la croissance pour expliquer la forme des otolithes.

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The ehu (*Etelis carbunculus*) is a red snapper of the family Lutjanidae. The Etelinae, one of the four subfamilies of Lutjanidae, comprise five genera: *Aphareus*, *Aprion*, *Etelis*, *Pristipomoides*, and *Randallichthys*. *Etelis carbunculus* are captured from the coast of Africa as far east as Hawaii and French Polynesia, as summarized by Allen (1985). They represent one of the principal species in the commercial hand-line catch from steep, rocky slopes at depths of 200–450 m.

Throughout the Pacific, *Etelis carbunculus* Cuvier (in Cuvier and Valenciennes 1828) has been referred to as *Etelis marshi*. Both Fourmanoir (1971) and Anderson (1981) pointed out that there were no significant morphological differences between specimens collected in the Pacific and those from the Seychelles Archipelago, previously described as *Etelis carbunculus*. Anderson's (1981) clarification of the morphological distinctions between *Etelis coruscans* and *Etelis carbunculus* further reduced confusion regarding the

geographic distribution and taxonomy of these two snappers. However, significant questions remain regarding the remarkable differences in the maximum size reached by *Etelis carbunculus* in different areas of the Pacific.

Fishermen and fisheries biologists have brought to light differences of over 50 cm in the maximum size of ehu captured in various regions of the northern and southern tropical Pacific. Fish measuring up to 90–110 cm (fork length) are found between the Cook Islands, Papua New Guinea, and the northeast coast of Australia (Brouard and Grandperrin 1985; Schaen et al. 1987; Lewis et al. 1988; Carlot and Nguyen 1989; Latu and Tulua;² Lokani et al.³; Nath and

²T. F. Latu and S. Tulua. Estimated maximum sustainable yield for Tonga deep bottom fishery. Contrib. Minist. Agric., Fish. and For., Fish. Div., Kingdom of Tonga, USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 15 p. (Manuscr.)

³P. Lokani, H. Pili, and G. Tiroba. Assessment of bottomfish resources of Papua New Guinea. USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 13 p. (Manuscr.)

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Sesewa⁴; Sua⁵). The largest fish reported in this region, at Vanuatu, weighed 12.2 kg and is estimated to have measured 127 cm (R. Grandperrin, ORSTOM, Centre de Noumea, Boite Postale A5, Noumea Cédex, Nouvelle Calédonie, pers. comm.). Maximum fish sizes for Hawaii and French Polynesia and in the range of 65–75 cm (Uchiyama and Tagami 1984; Wrobel 1985; Ralston and Kawamoto 1987), while ehu as large as 58 cm are rarely found in the region surrounding the Commonwealth of the Northern Marianas Islands (NMI) (Ralston and Williams 1988). Regional differences in maximum size between these stocks are evidence of their relative isolation, probably maintained by the distances and depths that separate them.

This study describes regional differences in otolith morphology in five areas of the Pacific. It began as an effort to evaluate the reasons for differences in maximum size. Regional otolith shape differences were so remarkable that they were first believed to be an indication of taxonomic differences between stocks. However, examination of regional specimens confirmed that all were *Etelis carbunculus*.

Materials and Methods

Fork lengths were recorded and sagittal otoliths collected from *Etelis carbunculus* captured at five sites throughout the Pacific between 100 and 400 m of depth. Otoliths were washed in 70% alcohol, dried, and stored in plastic envelopes. Following the measurements described below, sagittae were oven-dried and desiccated to a constant weight. A resin cast of the saccular lumen was made for a few fish of each size from Hawaii. Otoliths collected on a regional basis are summarized below:

Region	Year(s)	No. of otolith Pairs
Hawaiian Islands	1989	130
Fijian Islands	1987	26
	1989	109
French Polynesia	1985–86	42
	1989	32
NMI	1982	6
	1989	6
Vanuatu	1983	84

The growth focus is a useful point of reference, visible from the unsectioned otolith's concave lateral side. The view of the otolith from this side is referred to herein as the "lateral view" (see Fig. 1). To make the focus more apparent, otoliths were cleared using a glycerine and alcohol (2:3) mixture. The following proportions (Fig. 1) were recorded through a dissecting microscope from the video-relayed image (lateral view) of one of each pair of otoliths, using an optical software system designed by Biosonics, Inc. (1987): (1) distance from tip of rostrum to focus, (2) distance from postrostrum to focus, (3) distance from sulcus groove to tip of rostrum, (4) dorsal (i) and ventral (ii) width at the focus, (5) length from postrostrum to sulcus, (6) length from sulcus to tip of antirostrum, and (7) basal width of antirostrum.

⁴G. Nath and A. Sesewa. Progress report on fisheries research conducted on bottomfish stocks around the Fijian Republic. Contrib. Fish. Div., Minist. Primary Ind., Republic of Fiji, USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 21 p. (Manuscr.)

⁵T. Sua. Assessment of bottomfish resources of Western Samoa: an interim report. USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 20 p. (Manuscr.)

Otoliths were immobilized parallel to the field of view on a stand of polyurethane foam. The perimeter of each otolith was traced in a counterclockwise direction from two different perspectives, the ventral and lateral views. Each outline was digitized into a set of 128 virtual x, y coordinates, taken at equally spaced intervals along its perimeter, and a Fast Fourier Transform (FFT) of these points was taken of the form

$$(1) \quad R(\Theta) = A_0 + \sum_{n=1}^{128} A_n \cos(\Theta_n + \phi_n)$$

where the original particle representation and angular position ($R(\Theta)$) are decomposed into a standardized starting position (A_0) and 128 consecutive amplitude coefficients (A_n), with angular components (Θ_n) and slope components (ϕ_n). Rotational and size invariance was achieved by (1) dividing the amplitude coefficients by the amplitude of the first descriptor (A_1), (2) setting the A_0 frequency component to zero, and (3) iteratively rotating the shape in the frequency domain until an optimization function was maximized. The technique is outlined briefly in the Biosonics, Inc. (1987) manual and in more detail in references dealing with shape analysis (Alt 1962; Hu 1962; Clark 1981).

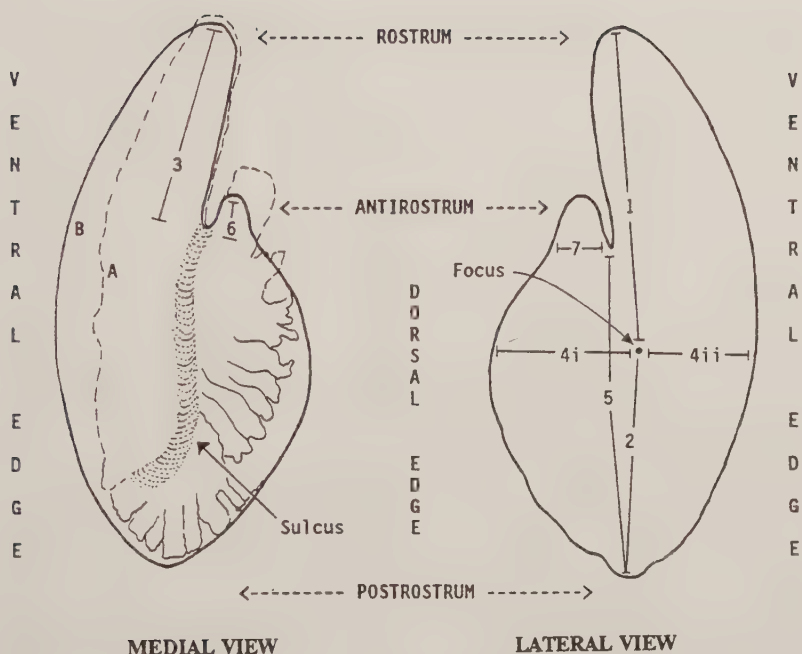
While the video-flattened lateral and ventral images made shape comparisons essentially two-dimensional, the ventral view provided an index of otolith curvature and the lateral silhouette showed much of the variation in overall shape. Two other characteristics recorded from the lateral view were the indices of (1) circularity, the perimeter squared divided by the area, and (2) rectangularity, the shape's area divided by the area of its minimum enclosing rectangle. Normalized Fourier descriptors, scaled indices of rectangularity and circularity, and ratios of linear proportions provided size-independent indices of otolith shape, allowing comparison of different sized otoliths.

The first 20 amplitudes ("harmonics") after A_0 and A_1 were used to characterize each FFT (normalization functions set $A_0 = 0$ and $A_1 = \text{unity}$ for all FFTs). The amplitude of each harmonic (A_n of equation 1) was calculated from Biosonics sine and cosine output (Castonguay et al. 1991) according to the relationship (Christopher and Waters 1974)

$$(2) \quad A_n = \sqrt{\sin_n^2 + \cos_n^2}$$

To evaluate whether otolith shape indices and weights varied as a function of fish size, otoliths were grouped by 10-cm fork length intervals and the indices were compared between size groups and regions using a Student–Newman–Keuls (SNK) means test (Sokal and Rohlf 1969). Regional nonhierarchical cluster analyses of linear proportions, harmonics, and shape indices were performed by the SAS "Fastclus" procedure (SAS Institute Inc. 1985), which clusters data into discrete groups by nearest centroid sorting using a k -means method (Anderberg 1973) on squared Euclidean distances (referred to hereinafter as NC cluster analysis).

Linear combinations of the multivariate regional shape characteristics were compared by canonical discriminant analyses (SAS "Candisc" procedure). The first and second canonical variables are maximally uncorrelated descriptors of the first- and second-order multiple regressions, respectively, used to characterize the sample in two dimensions. Interregional groupings were also evaluated using hierarchical average linkage cluster analyses (SAS "Cluster" procedure) on squared Euclidean distances. To avoid the disproportionate weighting of measurements made in different units or showing a wider range of variation, all cluster analyses were performed on data mat-



GENERAL SHAPE SHOWN FOR THE FOLLOWING REGIONS (MEDIAL VIEW)

A Fiji/Vanuatu

B Hawaii/NMI/French Polynesia

Symbol

----- (dashed line)

_____ (solid line)

FIG. 1. Medial and lateral views of the right sagittal otolith of the deep slope snapper (*Etelis carbunculus*).

rices standardized to dimensionless units with mean zero and standard deviation unity (Romesburg 1984).

Results

Dissection of fish skulls showed that the otolith abuts against the ventral and medial wall of each otic capsule (sacculus). Both the dorsal edge and outer lateral surface of the otolith are unconstrained by the bony walls of the otic capsule, extending into the macular lumen and held in place only by a gelatinous material. Resin casts of the saccular lumen for fish from Hawaii produced a mold almost identical to the ventral and medial surfaces of the otolith, while the casts were 4–6 times as thick and concave rather than convex like the otolith on their outer surface. Otoliths of small fish (<30 cm fork length) had some space within the otic capsule, even along the medial surface, while otoliths of medium-sized (30–50 cm) and large (>50 cm) fish fit more and more snugly into the sacculus, their shape increasingly molded to that of the ventral and medial surfaces of the otic capsule. The constraints on otolith shape imposed by the chamber that contains them may account for

much of the curvature and uniqueness of form which develops in the otoliths of large fish.

The relationship between fork length and linear otolith dimensions was examined by log-linear regression (Table 1). Although results obtained by this method are affected by the size range included in each regression, they are mentioned because of the interesting variation observed for all regions. Regression parameters for all six linear proportions (illustrated in Fig. 1) were allometric (b always less than 1) and varied in a regional and character-specific manner. While differences between regional samples are to be expected for several reasons, within-region variation in otolith growth rate along different axes (evidenced by within-region variation in b values) and in individual variability of these traits for the same otoliths (indicated by varying coefficients of determination, r^2) illustrates the complex three-dimensional nature of otolith growth. Regional regression parameters for otolith weight versus fork length are included in Table 1, along with predicted values of otolith weight within an intermediate fork length range, for the four regions that were well represented numerically. Predicted weight for Vanuatu was the lowest, followed in increasing order by Fiji, Hawaii, and French Polynesia.

TABLE 1. Allometric relationships for fork length versus otolith weights and linear dimensions.

Region	Otolith weight/ linear dimension	<i>a</i>	<i>b</i>	<i>n</i>	<i>r</i> ²
Hawaii	Otolith weight	4.383×10^{-6}	1.66	106	0.9512
	Rostral radius	222.2	0.56	128	0.7605
	Postrostral radius	165.6	0.58	128	0.8323
	Total length (at focus)	387.9	0.57	128	0.8949
	Dorsal radius	140.2	0.52	128	0.8134
	Total width (at focus)	217.4	0.55	128	0.8798
NMI	Postrostrum-sulcus length	479.3	0.48	128	0.8573
	Otolith weight	3.038×10^{-6}	1.74	9	0.8611
	Rostral radius	65.1	0.78	12	0.8193
	Postrostral radius	282.1	0.50	12	0.8511
	Total length (at focus)	255.6	0.65	12	0.8578
	Dorsal radius	443.4	0.32	12	0.3419
French Polynesia	Total width (at focus)	417.9	0.44	12	0.6415
	Postrostrum-sulcus length	388.1	0.52	12	0.7647
	Otolith weight	4.193×10^{-7}	2.10	67	0.9038
	Rostral radius	40.6	0.86	69	0.8464
	Postrostral radius	132.3	0.63	69	0.6510
	Total length (at focus)	138.2	0.76	69	0.8713
Fiji	Dorsal radius	80.0	0.63	69	0.6517
	Total width (at focus)	146.7	0.62	69	0.7608
	Postrostrum-sulcus length	477.3	0.49	69	0.7467
	Otolith weight	3.784×10^{-7}	2.017	105	0.8250
	Rostral radius	110.9	0.68	108	0.7774
	Postrostral radius	70.0	0.73	108	0.7510
Vanuatu	Total length (at focus)	179.2	0.70	108	0.8264
	Dorsal radius	88.6	0.58	108	0.4880
	Total width (at focus)	227.6	0.52	108	0.6381
	Postrostrum-sulcus length	278.0	0.58	108	0.6921
	Otolith weight	5.164×10^{-6}	1.60	82	0.8859
	Rostral radius	204.1	0.59	84	0.8718
	Postrostral radius	101.7	0.70	84	0.8895
	Total length (at focus)	295.7	0.63	84	0.9158
	Dorsal radius	188.3	0.48	84	0.7345
	Total width (at focus)	332.9	0.47	84	0.8081
	Postrostrum-sulcus length	449.3	0.51	84	0.8682

Equation: $y = ax^b$ where x = fork length (mm) and y = linear dimension (μ m) or dry weight (g)

Fork length (mm)	Predicted otolith weight (g)			
	Fiji	Vanuatu	Hawaii	French Polynesia
300	0.038	0.048	0.057	0.063
400	0.067	0.077	0.092	0.114
500	0.105	0.110	0.133	0.182
600	0.152	0.147	0.180	0.267
700	0.208	0.188	0.233	0.368

Regional differences in otolith morphology are a complex topic, since otoliths from all regions (except NMI for which the size range and number of samples were too small) showed significant differences in shape as a function of size. Table 2 summarizes the results of SNK means comparisons for each region for indices of otolith circularity and rectangularity. A circle would have the minimum circularity value ($4\pi = 12.57$), while a rectangle (or square) would have the maximum rectangularity value (unity). Tabled values indicate that large otoliths from all regions were both less circular and less rectangular than smaller ones. In some cases, decreasing circularity or rectangularity was apparent, but not statistically significant, due to a high sample-wide variability in shape and/or a small number of samples in some size groups. It is worth noting that the indices of circularity and rectangularity are not inverses, since

a circle and a square (or rectangle) have some symmetrical similarities. Furthermore, a shape's departure from rectangularity or circularity varies in two dimensions, while the numerical values of both shape indices vary linearly. This influences each index somewhat differently. Having an equal and larger number of otoliths from each size group would have helped clarify size-related shape differences, but the constraints of fishing and sampling opportunities worked out through cooperative long-distance agreements made this optimum difficult to achieve.

The ratios of linear measurements (Table 3) provided a good index of regional otolith shape variation. Data were pooled irrespective of size because they showed the same regional groupings (SNK, $\alpha \leq 0.01$), regardless of whether they were segregated by size. Regional groupings were similar to those seen for indices of circularity and rectangularity. The long and nar-

TABLE 2. Results of SNK means comparisons ($\alpha = 0.01$) for average otolith circularity and rectangularity as a function of size group by 10-cm intervals of fork length. Underlined values are not significantly different.

Region/characteristic	Length group (cm)					
	<30	31-40	41-50	51-60	61-70	71-80 >80
Mean circularity						(more circular)
Hawaii	23.45	<u>27.06</u>	<u>28.64</u>	31.13	<u>31.28</u>	
French Polynesia	<u>24.24</u>	<u>25.74</u>	<u>28.53</u>	36.08		
Fiji			<u>31.94</u>	<u>35.28</u>	38.80	<u>45.87</u> <u>46.71</u>
Vanuatu	<u>29.30</u>	<u>29.00</u>	<u>33.89</u>	<u>33.86</u>	<u>39.75</u>	<u>45.47</u> <u>42.98</u>
NMI	<u>26.32</u>	<u>27.97</u>	<u>29.97</u>			
Mean rectangularity						(more rectangular)
Hawaii	<u>0.6372</u>	<u>0.6202</u>	<u>0.6064</u>	<u>0.5966</u>	0.5381	
French Polynesia	<u>0.6453</u>	<u>0.6207</u>	<u>0.6122</u>	<u>0.5850</u>		
Fiji			0.5726	<u>0.5251</u>	0.5044	0.4999 0.4865
Vanuatu	<u>0.6003</u>	<u>0.5940</u>	0.5369	0.5304	<u>0.5238</u>	<u>0.4924</u> <u>0.4791</u>
NMI	<u>0.6455</u>	<u>0.6468</u>	<u>0.6439</u>			
Number of otoliths per size group						
Hawaii	42	28	37	11	1	
French Polynesia	17	40	10	2		
Fiji			8	35	33	19 13
Vanuatu	4	11	12	8	19	23 7
NMI	5	5	2			

TABLE 3. Results of SNK comparisons ($\alpha = 0.05$) between mean ratios of linear otolith measurements. Underlined values are not significantly different.

Ratios of otolith linear measurements	Regional mean (%)				
	Fiji	Vanuatu	NMI	Hawaii	French Polynesia
Rostral radius/Total length	52.47	<u>53.76</u>	<u>54.10</u>	<u>54.18</u>	<u>54.76</u>
Postrostral radius/total length	47.53	<u>46.24</u>	<u>45.90</u>	<u>45.82</u>	<u>45.24</u>
Postrostral radius/postrostrum-sulcus length	67.59	65.48	<u>63.45</u>	<u>62.75</u>	<u>61.63</u>
Total width/total length	39.65	41.66	<u>50.21</u>	<u>49.55</u>	<u>49.39</u>
Total width/postrostrum-sulcus length	56.42	58.88	<u>69.47</u>	<u>67.92</u>	<u>67.27</u>
Dorsal width/postrostrum-sulcus length	31.98	34.48	<u>37.59</u>	<u>37.36</u>	<u>37.00</u>
n for all tests	108	84	12	128	69

row otoliths from Fiji and Vanuatu segregated from those from the other regions, except for two instances where Vanuatu was grouped with the other three locations. Otoliths from Fiji and Vanuatu were significantly different for these proportions, while those from French Polynesia, Hawaii, and NMI could not be distinguished statistically.

Using the same six linear ratios and a seventh character, the ratio of the length from focus to tip of rostrum to that from postrostrum to sulcus (1:5 from Fig. 1), NC cluster analysis produced similar regional groupings (Table 4). The five-cluster-level partitioning of regional samples can be compared visually (table percentages in the last row of each section). Hawaiian and French Polynesian samples were primarily

represented in clusters 1 and 3 whereas otoliths from Fiji and Vanuatu were more abundant in clusters 4 and 5. The sample size for NMI was very small, but these otoliths were mostly grouped into clusters 1 and 3 with those from Hawaii and French Polynesia.

The A_{2-22} harmonics (ventral and lateral views) formed similar regional NC clusters (Table 5). Since the results were consistent, regardless of size category, data were again pooled. Whatever index of shape was chosen, otoliths from Fiji and Vanuatu were segregated from those from Hawaii, French Polynesia, and NMI. As might be expected, FFT shapes produced more discrete clusters than linear proportions, and these were more well defined for the lateral than for the ventral view.

TABLE 4. Regional nearest centroids clusters of the ratios of seven otolith traits for deep slope red snapper. Data presented as frequency, overall %, row %, and column %.

Cluster	Region					No. per cluster and %
	Fiji	Hawaii	NMI	French Polynesia	Vanuatu	
1	1	71	6	35	6	119
	0.25	17.71	1.50	8.73	1.50	29.68
	0.84	59.66	5.04	29.41	5.04	
	0.93	55.47	50.00	50.72	7.14	
2	6	3		2	3	14
	1.50	0.75		0.50	0.75	3.49
	42.86	21.43		14.29	21.43	
	5.56	2.34		2.90	3.57	
3	3	37	4	20	2	66
	0.75	9.23	1.00	4.99	0.50	16.46
	4.55	56.06	6.06	30.30	3.03	
	2.78	28.91	33.33	28.99	2.38	
4	48	2	1		20	71
	11.97	0.50	0.25		4.99	17.71
	67.61	2.82	1.41		28.17	
	44.44	1.56	8.33		23.81	
5	50	15	1	12	53	131
	12.47	3.74	0.25	2.99	13.22	32.67
	38.17	11.45	0.76	9.16	40.46	
	46.30	11.72	8.33	17.39	63.10	
Total n	108	128	12	69	84	401
%	26.93	31.92	2.99	17.21	20.95	100.00

Pseudo F statistic = 151.8

χ^2 (df 24, $P < 0.0001$) = 632.9

Ratios of otolith linear proportions	Corresponding numerical references from Fig. 1
Rostral radius/total length	1:(1 + 2)
Rostral radius/postrostrum-sulcus length	1:5
Postrostral radius/total length	2:(1 + 2)
Postrostral radius/postrostrum-sulcus length	2:5
Total width/total length	(4i + 4ii):(1 + 2)
Total width/postrostrum-sulcus length	(4i + 4ii):5
Dorsal width/postrostrum-sulcus length	4i:5

Canonical discriminant analyses (CDA) and hierarchical clustering were designed to evaluate between-region shape affinities. CDA were used to represent multidimensional shape vectors in a single plane, allowing both quantitative and qualitative assessment of the proximity and content of specific clusters. Plots of canonical discriminant functions from both types of shape indices (Fig. 2) show two principal clusters connected by a transition zone. The cluster group nearest the origin and the y-axis primarily contains otoliths from Hawaii and French Polynesia (with a few from NMI). The transition zone and the cluster closer to the upper range of the x-axis (and widely dispersed along the y-axis) are mainly composed of otoliths from Fiji and Vanuatu. The results are shown for six linear dimensions, circularity, and rectangularity (Fig. 2A) and for the first 10 harmonic descriptors (Fig. 2B, lateral view).

Using regional mean values for the three sets of traits listed in Tables 4 and 5, hierarchical cluster analyses linked otolith shapes from French Polynesia, NMI, and Hawaii and distinguished them from those from Vanuatu and Fiji (Fig. 3). FFT data show a greater definition between regions, since harmonics represent a more sensitive shape indicator.

TABLE 5. Regional groups by nearest centroid clustering of 20 otolith FFT harmonic amplitudes (A_{2-22}). Data presented as frequency, overall %, row %, and column %.

Cluster	Region					No. per cluster and %
	Fiji	Hawaii	NMI	French Polynesia	Vanuatu	
<i>Lateral view</i>						
1	5				3	8
	1.32				0.79	2.11
	62.50				37.50	
	4.85				3.16	
2	21				20	41
	5.53				5.26	10.79
	51.22				48.78	
	20.39				21.05	
3	56	24	2	5	44	131
	14.74	6.32	0.53	1.32	11.58	34.47
	42.75	18.32	1.53	3.82	33.59	
	54.37	18.60	16.67	12.20	46.32	
4	12				7	19
	3.16				1.84	5.00
	63.16				36.84	
	11.65				7.37	
5	9	105	10	36	21	181
	2.37	27.63	2.63	9.47	5.53	47.63
	4.97	58.01	5.52	19.89	11.60	
	8.74	81.40	83.33	87.80	22.11	
Total n	103	129	12	41	95	380
%	27.11	33.95	3.16	10.79	25.00	100.00

Pseudo F statistic = 201.9

χ^2 (df 24, $P < 0.0001$) = 778.5

Ventral view						
1	35	9	1	2	28	75
	9.19	2.36	0.26	0.52	7.35	19.69
	46.67	12.00	1.33	2.67	37.33	
	33.65	7.03	8.33	4.76	29.47	
2		1				1
		0.26				0.26
		10.000				
		0.78				
3		4		2		6
		1.05		0.52		1.57
		66.67		33.33		
		3.12	4.76			
4	63	44	3	9	58	177
	16.54	11.55	0.79	2.36	15.22	46.46
	35.59	24.86	1.69	5.08	32.77	
	60.58	34.38	25.00	21.43	61.05	
5	6	70	8	29	9	122
	1.57	18.37	2.10	7.61	2.36	32.02
	4.92	57.38	6.56	23.77	7.38	
	5.77	54.69	66.67	69.05	9.47	
Total n	104	128	12	42	95	381
%	27.30	33.60	3.15	11.02	24.93	100.00

Pseudo F statistic = 250.4

χ^2 (df 24, $P < 0.0001$) = 653.9

Discussion

This study summarizes evidence of regional and local variation in morphology of the otoliths of *Etelis carbunculus*. Rapid

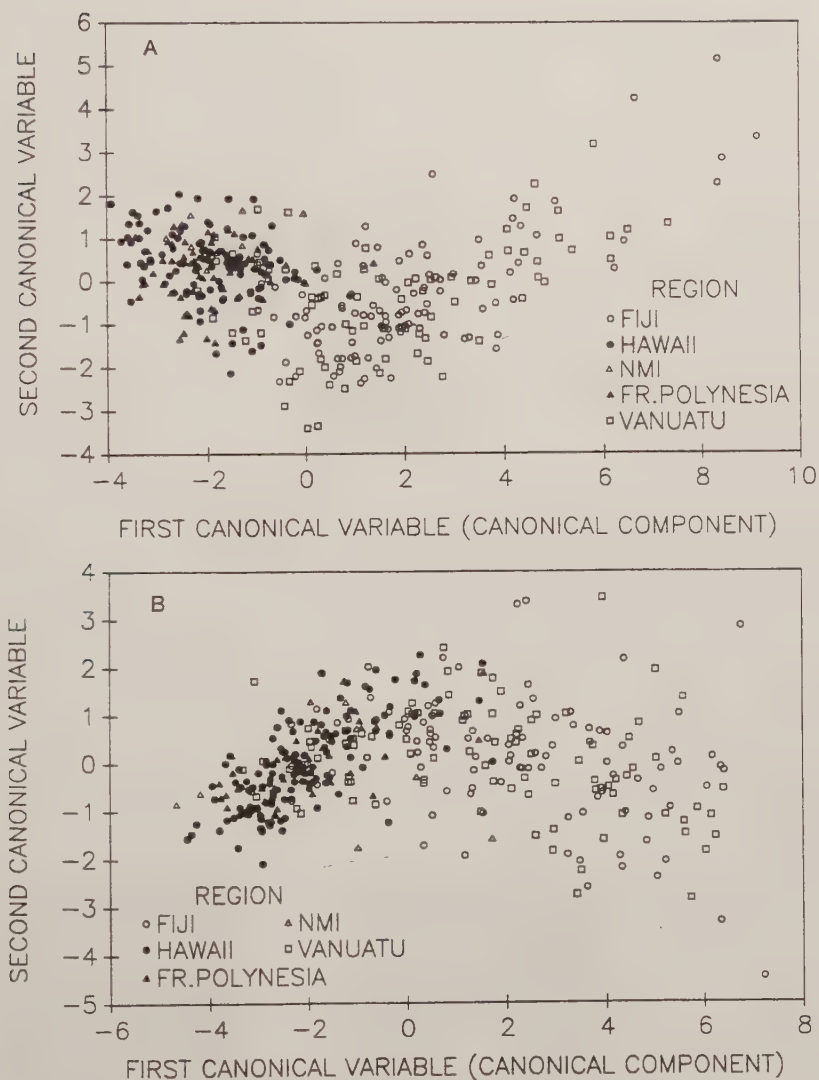


FIG. 2. Plot of canonical discriminant functions from (A) seven linear dimensions, circularity, and rectangularity and (B) 10 FFT harmonics (lateral view) for otoliths of the red snapper.

and localized declines in abundance of this species throughout the Pacific in response to fishing pressure (Schaan et al. 1987; Ralston and Kawamoto 1987; Carlot and Cillaurren⁶; Latu and Tulua (see footnote 2); Nath and Sesewa (see footnote 4)) are an indication of low rates of migration and relatively slow growth which, together with the distance and depth between suitable habitat, lend themselves to the development of regional variation.

Regional differences in growth rate may be a primary factor in the development of differences in otolith shape. The simi-

larity in shape of otoliths from such widely separated regions as NMI, French Polynesia, and the Hawaiian Islands suggests that growth rate represents an important component of otolith shape. These regions have slow or limited growth in common and had thicker, heavier, and more rounded otoliths. Available estimates (Uchida et al. 1982; Brouard et al. 1983; Brouard and Gradperrin 1985; Ralston and Kawamoto 1987; Ralston and Williams 1988; Carlot and Nguyen 1989) indicate that ehu from the southwestern Pacific grow considerably faster than those from Hawaii, NMI, and French Polynesia. Fish from NMI may initially grow at a similar rate to those from the southwestern region (Smith and Kostlan 1991), but do not reach comparably large sizes. Differences in otolith shape may be mediated through differences in the orientation and packing in

⁶A. H. Carlot and E. Cillaurren. Present status in yield assessment for deep bottom fishery in Vanuatu. Contrib. Fish. Dep. and ORSTOM, Port Vila, Vanuatu, USAID/NMFS Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 17 p. (Manuscr.)

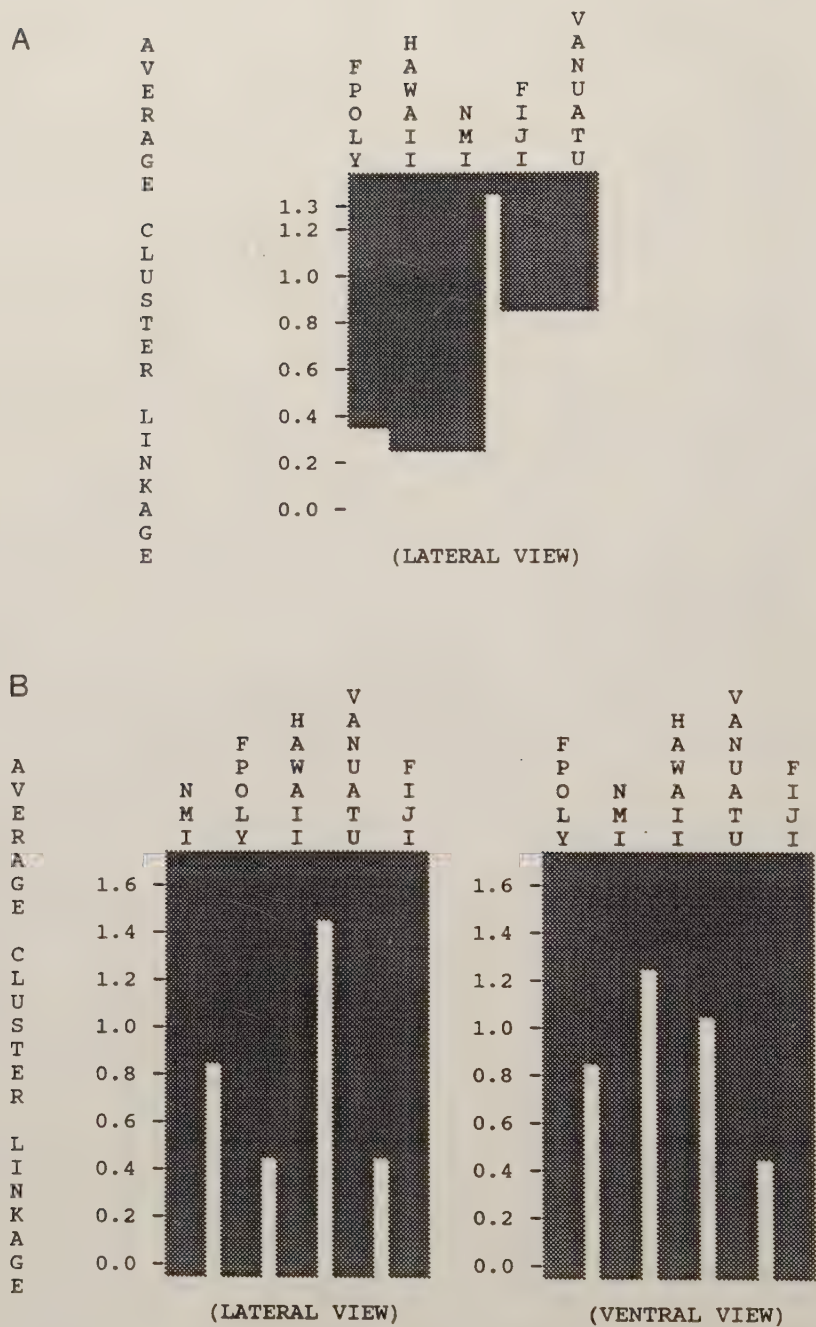


FIG. 3. Hierarchical clusters (cluster dendograms in the style of Johnson 1967) of regional otolith samples based on (A) six linear proportions, circularity, and rectangularity and (B) 20 harmonics.

the otolith crystal, which could easily be influenced by the rate of crystalline growth.

Growth-related differences in linear otolith proportions have been described for other species (Reznick et al. 1989; Secor and Dean 1989). Gaemers and Crapon de Crapona (1986) referred to a sexual dimorphism in otoliths of haplochromines. Faster growing males of these cichlids have more elongate and thinner otoliths. Gaudie et al.⁷ described differences in otolith shape as a function of parasite load for orange roughy (*Hoplostethus atlanticus*). Slow-growing parasitized fish had thicker and wider otoliths. Wilson (1985), describing compensatory depth-related differences in otolith shape for macrourids from the Atlantic and Pacific oceans, found that otoliths were either long and thin or short, wide, and thick. The shape differences noted by Wilson may be attributable to regional and depth-related differences in temperature and/or fish growth rates.

Data compiled by the National Oceanographic Data Center (NODC) (1989) show that mean temperatures at 150–400 m, where ehu are found, are 2–6° lower for Hawaii and NMI than for Fiji and Vanuatu. Temperatures for French Polynesia were 2–3° lower between 275 and 400 m, but were comparable with Fiji and Vanuatu above that depth. Uncoupling of somatic and otolith growth rates as a function of temperature has been described in the literature (Mosegaard et al. 1988). Whether differences in temperature affect otolith shapes directly or through temperature-related constraints on somatic growth cannot be determined from this study. Other factors (such as differences in feeding and food availability between locations) may also be responsible for regional variation in size. Information on habitat, population biology, and morphology of *Etelis carbunculus* must eventually be tied together to evaluate the causes of regional size and shape differences in this species.

Ehu provide an illustration of the continuous changes in shape taking place in otoliths throughout the life cycle. Changes in otolith shape in larval fishes are well known, but post-juvenile shape differences are rarely mentioned in the literature. These changes may be related to shifts in the metabolic rate (Gaudie 1990) as fish mature.

This summary of otolith measurements in several dimensions makes it clear that the otolith does not grow at a constant rate along all axes. For this reason, several planes of sectioning must be considered before attempting to interpret growth from seasonal, annual, or daily growth marks obtained from sections of the otolith (Radtko 1987). Due to the changing relationship between fish age (or size) and otolith shape, regressions of fish length versus linear otolith measurements in any dimension will vary as a function of the size range and number of fish from which data are obtained. The complexity of considerations to be made in selecting a representative size range and number of samples for a given population is illustrated by the fact that the foregoing comparisons between fish of different sizes were affected by size-specific differences in otolith shape, despite the fact that shape indices were scaled to size. Thus, the importance of careful planning to collect a representative sample for the determination of growth parameters must be stressed.

Otolith morphology has long been used in stock differentiation (Einarsson 1951; Zijlstra 1958; Kotthaus 1961; Messieh 1972; Postuma 1974), but recently, otoliths have become

increasingly popular for their timekeeping properties. As Fourier series (Bird et al. 1986; Gaudie and Nelson 1990; Castonguay et al. 1991), scanning electron microscopy (Davies et al. 1988; Gaudie et al. 1990), and other methods make it increasingly feasible to discern differences in otolith shape and molecular structure, researchers have begun to point out a wide range of inter- and intrapopulational differences in otolith shape. Differences in the morphology of otoliths of *Etelis carbunculus* were first believed to be an indication of taxonomic differences in stocks. However, while regional stocks fit the species description, otolith morphology proved to be quite varied and complex. The three-dimensional variation in otolith growth rate described herein represents another indication that growth estimation from single-plane sectioning may someday be viewed as an oversimplification. Since a better understanding of the determinants of otolith structure is paramount to the interpretation of age and growth in fishes, as well as to discussions of stock differentiation and otolith taxonomy, these findings may eventually have more far-reaching applications.

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LIFE-STAGE DURATION AND SURVIVAL PARAMETERS AS RELATED TO INTERDECADAL POPULATION VARIABILITY IN PACIFIC SARDINE

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ABSTRACT

Surveys in the Southern California Bight have shown rapid increases in the spawning rate of Pacific sardine over the past decade. We found simple deterministic population models to be useful for examining the rates of change observed in the sardine population. We first describe the "best guess" parameters of an equilibrium sardine population with the Leslie matrix model. From this we determine that small changes in annual mortality rate of the O-group impose high rates of change in the population. We then erect a Lefkovich matrix model, which uses life stages rather than ages, to emphasize the parameters of the early life stages. From this study, we can specify the range of growth rates and the changes in survival rates for each developmental stage, as well as the adult parameters required to evaluate the observed rates of change.

Changes in egg production rates imply important changes in the sardine population. Therefore, examination of these rates of change can offer insight into the frequency and precision of population assessment and recruitment prediction required for effective management of fisheries on sardines and other stocks.

RESUMEN

Reconocimientos en la Cuenca del Sur de California han revelado que en la década pasada la tasa de desove de la sardina del Pacífico mostró un incremento pronunciado. Encontramos que modelos poblacionales deterministas simples son útiles para investigar las tasas de cambio observadas en poblaciones de sardinas. Describimos primero los parámetros que juzgamos más atinados de una población de sardina en equilibrio con un modelo de matrices de Leslie; determinamos que pequeños cambios en la tasa de mortalidad anual del grupo de edad cero producen altas tasas de cambio en la población. Continuamos con la elaboración de un modelo de matrices de Lefkovich, que al considerar fases vitales en vez de edades, hace hincapié en los parámetros de los estadios vitales tempranos. A partir de

este estudio, podemos especificar el rango de las tasas de crecimiento, los cambios en las tasas de sobrevivencia para cada fase de desarrollo y los parámetros de los estadios adultos requeridos para evaluar las tasas de cambio observadas.

Cambios en las tasas de producción de huevos llevan consigo cambios importantes en la población de sardinas. Consecuentemente la investigación de tales tasas podría ayudar a discernir la frecuencia y precisión de la evaluación de la población, así como la predicción del reclutamiento, elementos requeridos para un manejo efectivo de las pesquerías de sardinas y otros stocks.

INTRODUCTION

The current recovery of Pacific sardine was predicted by Murphy (1967) based on a deterministic population model, and by Lenarz (1971), who used a stochastic model and incorporated autocorrelation of recruitment success. Records of the Pacific sardine fishery begin in the late 1800s (Schaefer et al. 1951), with small catches being used for bait in the rockfish fishery, and for canning. During World War I the fishery grew continuously at a rate of about 14% per year, doubling every five years. Brief deviations from the growth of the fishery were largely attributed to economic factors (Schaefer et al. 1951). The catch was chiefly landed in California, but fisheries extended northward to British Columbia.

The growth rate of the fishery slowed after the mid 1930s, and a succession of collapses began in 1945–47. California landings fell below the 1916 values in the 1961–62 season (Ahlstrom and Radovich 1970), where they have remained through 1991. California legislation in 1967 and 1973 prohibited the landing of sardines for any purpose and prevented the sale of incidental catches. The 1973 legislation stipulated that a 1,000-ton fishery could start as soon as the spawning biomass exceeded 20,000 tons; thus a small fishery began in 1986 and continues to grow (Wolf et al. 1987).

There has been relatively little directed research on the Pacific sardine population off California since

the decline of the 1960s; most of the research was reviewed by Ahlstrom and Radovich (1970). Smith (1972) updated and revised Ahlstrom's (1966) egg and larval time series. MacCall (1979) updated and revised Murphy's (1966) population data. Soutar and Isaacs (1974) augmented the record of sardine and other fish scales in the anaerobic varved sediments off California and added a record from Baja California (Soutar 1967; Soutar and Isaacs 1969). Lasker (1970) estimated the use of zooplankton energy by the historical sardine population.

The recovery of the sardine population was first detected in 1979, through surveys by the Ichthyoplankton Coastal and Harbor Studies in waters shallower than 40 meters off Santa Monica Bay, Palos Verdes, and Seal Beach in southern California. These bimonthly field studies were sponsored by the Southern California Edison Co. and NOAA Sea Grant and were staffed by the Los Angeles County Museum and the Institute for Marine and Coastal Studies of the University of Southern California (Brewer et al. 1980; Brewer and Smith 1982; Lavenberg et al. 1987). Wolf and Smith (1985, 1986) estimated the spawning biomass from the spawning area in 1985.

Sardine and anchovy fisheries constitute a relatively large fraction of the fluctuations in global catch (Murphy 1977; Smith 1985; Lluch et al. 1989). Although variations in recruitment are large for sardine and anchovy stocks, the major changes appear to be long term. Thus the "overfishing problem" is complicated by the "recruitment problem" and the "regime problem."

In the near future we plan to issue a series of matrix models for schooling coastal pelagic fishes. This paper concerns the relationship between population parameters and observed rates of change in the sardine population. We also plan to produce papers on the sensitivity of sardine and anchovy population size to changes in parameters based on Smith (1985) and Smith, Lo, and Butler (1991). In addition, we plan to compare the errors of estimation of the abundance of life stages with interannual changes in population size.

In this paper we use the recent remarkable increases in Pacific sardine egg abundance off southern California to pose questions about the causes of the increase. Is the current increase due to migration of sardine stocks from other habitats to the southern California area? How does the increase of spawning off southern California compare to the increase off Japan? Is the increase due merely to the fishing moratorium? Has the increase resulted from the decline in natural predators? Have other population param-

eters changed? Can normal fluctuations in recruitment rates be detected in time to improve fisheries management? Can critical changes in the recruitment rate be predicted from observations of the physical and biological environment of the sardine?

It is the purpose of this paper to explore some characteristics of Pacific sardine with respect to the observed changes in population size. We have prepared similar estimates for the northern anchovy (Smith 1985; Smith et al. 1991). First we postulate values for stage survival, growth, and reproduction parameters. We then determine which features of the population are most likely to control the sardine's reproductive success. Lastly, we describe the related features of the biological and physical environment. Although there are serious reservations surrounding the use of the simple Leslie (1945) and Lefkovich (1965) matrix models for projecting population (Caswell 1989; Seber 1973), tractable methods have been developed for evaluating and extending these models (DeRoos et al. 1992). For this stage of our research, we chose the simplicity and flexibility of the Leslie (Vaughn and Sails 1976) and Lefkovich (Crouse et al. 1987) matrix models.

METHODS

Abundance estimates for sardine eggs arise from quantitative techniques that were established in 1938 (Sette and Ahlstrom 1948) and that have not changed with respect to sardine eggs since then. Sardine population parameters have been selected from Butler (1987). Where values are missing for sardine, we used analogous parameters for the same stage of anchovy (Smith 1985; Lo 1986; Lo et al. 1989; Smith et al. 1991).

The egg time series, from representative surveys selected from 1957 to 1991, is shown in table 1, which lists the number of sardine eggs of all ages per 10 square meters of sea surface between CalCOFI line 76 (at times called 77 or 76.7) and line 94 (usually called 93 or 93.3). Data from all tows taken from January to June at CalCOFI stations 26 to 70 were used. Surveys were conducted from two to five times in the six-month period. The maximum number of stations was 293 in 1975; the minimum number was 77 in 1990 and 1991. The data reported in table 1 represent two series of egg abundances on the decadal scale with relatively even rates of decline (1957-69) or increase (1975-91).

Scale-deposition rates from the fossil record in the Santa Barbara Basin (Soutar and Isaacs 1974; Smith 1978; Smith and Moser 1988) are shown in table 2. A Velleman nonparametric, robust, resistant smoother (Velleman 1980; Velleman and Hoagland 1981; Min-

TABLE 1
Time Series of Sardine Eggs off Southern California

Year	Eggs per 10 m ² sea surface
1957	22.65
1958	69.02
1959	143.85
1960	95.36
1961	12.85
1962	1.35
1963	11.29
1964	0.61
1965	3.66
1966	1.54
1969	0.27
1972	0
1975	2.43
1978	0.38
1981	0.87
1984	3.47
1985	9.27
1986	3.25
1987	16.14
1988	34.20
1989	53.34
1990	67.29
1991	137.11

TABLE 2
Smoothed Time Series of the Soutar-Isaacs* Sardine-Scale Series from the Santa Barbara Basin

Central year	Scale deposition	Smoothed ^b rates	Series
1812	2.44	2.44	R1
1817	2.58	2.58	R1
1822	3.72	2.87	R1
1827	1.29	3.18	R1
1832	5.15	3.42	R1
1837	3.11	3.81	R1
1842	3.74	4.51	R1
1847	7.72	5.64	R1
1852	5.11	6.70	R1
1857	15.19	7.07	R1
1862	8.47	5.96	F1
1867	0.62	3.10	F1
1872	0.25	0.71	F1
1877	0.00	0.08	F1
1882	1.00	0.98	R2
1887	1.49	3.30	R2
1892	8.72	5.24	R2
1897	12.08	5.71	R2
1902	4.61	5.50	F2
1907	1.99	5.18	F2
1912	2.99	4.93	F2
1917	5.85	4.72	F2
1922	6.85	4.61	F2
1927	3.99	4.27	F2
1932	1.99	3.22	F3
1937	3.11	1.88	F3
1942	0.50	0.84	F3
1947	0.37	0.29	F3
1952	0.00	0.08	F3
1957	0.00	0.02	F4
1962	0.32	0.00	F4
1967	0.00	0.00	F4

*Soutar and Isaacs 1974

^bVelleman (1980) nonparametric resistant smoother

itab 1989) was used to define secular (long-term) trends and changes in trend. This smoother replaces each value by the median of the values immediately before and after it. Medians of 2, 3, 4, and 5 consecutive values were used in this smoother. Following each median smoother, a weighted running average of each value and the values immediately preceding and following is assembled, with the point value being given twice the weight of the adjacent values. Special methods are used to smooth the ends of the data sequence.

Secular change rates for all time periods were estimated by Marquardt algorithm nonlinear least squares fitted to an exponential function (Saila et al. 1988). We used the same procedure to extract secular rates of change from graphics published by Murphy (1967) and Lenarz (1971). The absence of the actual values in the latter cases should not be an impediment, since the data were based on theory and simulation in both cases.

We used a Leslie matrix of 13 year classes (Leslie 1945; Vaughn and Saila 1976) to estimate the survival rate during the first year of sardine life from the age-fecundity relation (table 3) and the adult survival rates from Butler (1987: table 2). We set the adult annual survival rate at a constant 0.67 (instantaneous mortality rate of 0.4 yr⁻¹) (table 4).

The Lefkovich matrix also included 13 life stages (Crouse et al. 1987; Smith et al. 1991). Rather than using individual year classes as in the Leslie matrix, we assembled the adult year classes into only 3 stages: early adult, adult, and late adult. The fecundity of the adult stages is derived from the biomass-weighted fecundity of the year classes encompassed by the stages. Daily instantaneous mortality rates and durations (days) of stages are given in table 5. Each rate shown is varied individually while the other rates are held constant. We divided the early

TABLE 3
Sardine Fecundity Schedule

Age	Weight(g)	Eggs/g/batch	Batches/yr ^a	Eggs/female/year
1	52.7	0	0	0
2	93	257	4	95604
3	123	257	8	252888
4	152	257	12	468768
5	170	257	15	655350
6	183	257	17	799527
7	193	257	19	942419
8	202	257	20	1038280
9	205	257	20	1053700
10	205	257	21	1106385
11	205	257	21	1106385
12	205	257	22	1159070
13	205	257	23	1211755

^aButler 1987 (postulated by analogy to anchovy) and Smith et al. 1991.

TABLE 4
Projection Matrices of Leslie (1945) and Lefkovich (1965)

Leslie Age-Based Matrix							
f_0	f_1	f_2	f_3	$\cdot$	$\cdot$	$\cdot$	f_n
p_0	0	0	0	$\cdot$	$\cdot$	$\cdot$	0
0	p_1	0	0	$\cdot$	$\cdot$	$\cdot$	0
0	0	p_2	0	$\cdot$	$\cdot$	$\cdot$	0
0	0	0	p_3	$\cdot$	$\cdot$	$\cdot$	0
$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	0
$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	0
$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	0
0	0	0	0	0	0	p_{n-1}	0
Lefkovich Size- or Stage-Based Matrix							
f_0	f_1	f_2	f_3	$\cdot$	$\cdot$	$\cdot$	f_n
g_0	p_1	0	0	$\cdot$	$\cdot$	$\cdot$	0
0	g_1	p_2	0	$\cdot$	$\cdot$	$\cdot$	0
0	0	g_2	p_3	$\cdot$	$\cdot$	$\cdot$	0
0	0	0	g_3	$\cdot$	$\cdot$	$\cdot$	0
$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	0
$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	0
$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	$\cdot$	0
0	0	0	0	0	0	p_{n-1}	0
0	0	0	0	0	0	g_{n-1}	p_n

f is the fecundity per fish per unit of time by age for Leslie matrix and for stage in the Lefkovich matrix.
 p is the probability of survival to the next age for Leslie matrix, and the probability of survival in the stage for the Lefkovich matrix.
 g is the probability of survival and growth into the next stage.

life history of the sardine into the following stages: egg, yolk-sac larva, first-feeding larva, late larva, early juvenile, juvenile I, juvenile II, juvenile III, juvenile IV, and pre-recruit. After we established best estimates for the parameters, we changed the least-known estimates—juvenile I and II—by trial

TABLE 5
Postulated Parameters of the Sardine Life Cycle

Stage name	Duration (days)	Instantaneous mortality rate (daily)	Eggs per fish per day
Egg	3	0.3	0
Yolk-sac larva	4	0.3	0
Early larva	11	0.14	0
Late larva	42	0.0556	0
Early juvenile	25	0.0365	0
Juvenile I	100	0.0239	0
Juvenile II	142	0.0140	0
Juvenile III	170	0.0025	0
Juvenile IV	170	0.0021	0
Pre-recruit	175	0.0021	0
Early adult	381	0.00178	169.72
Adult	663	0.00178	462.31
Late adult	2773	0.00178	1258.91

and error to achieve a neutral population growth rate ($\lambda = 1$).

Considering the range of rates of secular change in table 6, we established alternative population growth rates of $\lambda = 0.7$ and $\lambda = 1.3$. We then changed each population parameter, such as individual growth rate or mortality rate, until the population growth rate matched the $\lambda = 0.7$ or $\lambda = 1.3$ value or until the parameter went to zero or an unreasonable value. We manipulated the early life stages, keeping the natural mortality constant at 0.4 yr^{-1} and the fishing mortality at 0.25 yr^{-1} . In this form we would not expect great differences in re-

TABLE 6
Examples of Secular Changes in Sardine Population Size

Category	Time span (years)	r^a	λ^b	References
Theoretical				
Murphy	0–24	0.184	1.202	Murphy 1967
Lenarz	0–16	0.168	1.183	Lenarz 1971
Santa Barbara Basin scales				
Table 2 R1	1810–1860	0.027	1.028	
Table 2 F1	1860–1880	–0.103	0.902	
Table 2 R2	1880–1900	0.088	1.092	
Table 2 F2	1900–1930	–0.009	0.991	
Table 2 F3	1930–1955	–0.099	0.906	
Table 2 F4	1955–1970	–0.335	0.715	
Southern California				
Eggs	1975–1991	0.523	1.687	This paper
Eggs	1957–1969	–0.193	0.824	This paper
Recruits	1932–1964	–0.071	0.931	Murphy 1966 & MacCall 1979
Spawners	1932–1965	–0.108	0.898	Murphy 1966 & MacCall 1979
Benguela Current				
Spawners	1966–1982	–0.245	0.783	Crawford et al. 1983
Humboldt Current				
Spawners	1974–1981	0.126	1.134	Serra 1983
Kuroshio				
Eggs	1970–1978	0.488	1.514	Watanabe 1983

r^a = annual intrinsic exponential rate of population change.

λ^b = annual rate of sardine population growth (e^r).

sults from the Lefkovitch stage-and-size-specific matrix and the Leslie age-specific matrix.

RESULTS

The extreme rates of change indicated by all methods of estimating biomass, scale-deposition rates, standing crop of eggs, and virtual population incorporate not only the real rates of change of the population but also errors in the estimation of population levels and changes in age composition. Since many forms of error are multiplicative, the asymmetry in table 6—i.e., high rates of increase exceed rates of decrease—could either be a characteristic of sardines and anchovies or merely an expression of the errors of estimation. Although we report the maximum and minimum rates of increase as results, we have narrowed the range of subsequent tests of population parameters to explore only the range $\lambda = 0.7$ to $\lambda = 1.3$. The lower λ is somewhat more interesting for fishery management.

The fastest rate of secular increase occurred in the standing crop of eggs. By 1991 there was an average standing crop of 137 sardine eggs per ten square meters. In 1975 the mean concentration of eggs in the same area was fewer than 3 per ten square meters. The average growth rate since 1975 is an instantaneous rate of 0.523 yr^{-1} (SE 0.038). The equivalent λ is 1.687. Even with errors in estimation of values and estimation of slope we would expect this result to be above a λ of 1.3, meaning that the spawning rate was expanding at more than 30% per year. The effects of changed reproductive parameters on estimated biomass are explored below.

The fastest rates of secular decline examined for this paper were in the scale-deposition rate from 1955 to 1970 (table 6), in Namibian sardine (*Sardinops ocellata*) spawners (Crawford et al. 1983), and in Pacific sardine spawners from 1932 to 1964 and recruits in 1965 off southern California (Murphy 1966; MacCall 1979). The California declines approached 20% to 30% per year, and were accompanied by many adults and some juveniles being taken by an active fishery.

Leslie Matrix

The fastest rates of increase cannot be obtained in theory from changing from a fishing instantaneous mortality of 0.25 yr^{-1} to a moratorium (0 yr^{-1}). The fastest population increase expected from a moratorium on fishing is about 20% per year (table 7A). The highest secular rate of increase from the prefishery scale-deposition rates was about 10% per year from 1880 to 1900 (table 6).

TABLE 7
Sardine Life-History Parameters Representing No Population Change, 30% Annual Decline, and 30% Annual Growth

	$\lambda = 1$	$\lambda = 0.7$	$\lambda = 1.3$
A. Leslie matrix (13)			
Fishing mortality	0.25	0.72	<0.0*
O-group survival $S(1, 0)$	6.51E-06	9.90E-07	1.84E-05
O-group mortality $Z(\text{yr}^{-1})$	11.94	13.83	10.91
O-group mortality $Z(\text{d}^{-1})$	0.033	0.038	0.030
Fecundity (batches yr^{-1})	23	3.50	65
Batch fecundity (eggs gm^{-1})	257	39	725
B. Lefkovitch matrix (13)			
Egg (spawn to hatch)			
IMR (d^{-1})	0.3	0.887	0.0003
Duration (d)	3	8.875	0.01
Yolk-sac larva (hatch–4 mm)			
IMR (d^{-1})	0.3	0.7401	0.0752
Duration (d)	4	9.875	1.0089
Early larva (4–10 mm)			
IMR (d^{-1})	0.14	0.2999	0.0582
Duration (d)	11	23.59	4.593
Late larva (10–35 mm)			
IMR (d^{-1})	0.0556	0.0974	0.0341
Duration (d)	42	73.7	25.87
Early juvenile (35–60 mm)			
IMR (d^{-1})	0.0365	0.10665	0.00032
Duration (d)	25	73.52	0.69
Juvenile I (60–85 mm)			
IMR (d^{-1})	0.0239	0.04137	0.014815
Duration (d)	100	173.85	62.56
Juvenile II (85–110 mm)			
IMR (d^{-1})	.0140	0.02623	.00755
Duration (d)	142	268.4	78.51
Juvenile III (110–135 mm)			
IMR (d^{-1})	.002495	.012427	— ^b
Duration (d)	170	996	—
Juvenile IV (135–160 mm)			
IMR (d^{-1})	.0021	0.01201	—
Duration (d)	170	1203	—
Pre-recruit (160–185 mm)			
IMR (d^{-1})	.0021	0.011715	—
Duration (d)	175	1206.5	—
Early adult (185–210 mm)			
IMR (d^{-1})	.0018	0.0064	<0 ^c
Duration (d)	381	>3653	<1
Fecundity (d^{-1})	169.6882	—	1108.9
Adult			
IMR (d^{-1})	.0018	0.0066	<0 ^d
Duration (d)	663	>3653	<1
Fecundity (d^{-1})	462.2455	—	2145.7
Late adult			
IMR (d^{-1})	.0018	>0.0274	<0 ^e
Duration (d)	2773	>3653	<1
Fecundity (d^{-1})	1238.6	—	6595.5

*When fishing mortality is 0 (moratorium) $\lambda = 1.214$.

^bWhen no value is mathematically possible the symbol — is used.

^cWhen fishing mortality is 0, $\lambda = 1.0625$.

^dWhen fishing mortality is 0, $\lambda = 1.0725$.

^eWhen fishing mortality is 0, $\lambda = 1.0513$.

Variation in O-group mortality rate can effect either a 30% increase or decrease in λ . A decline of this magnitude would result from the first-year survivorship of 9.90×10^{-7} from each egg spawned, or 1 survivor for each 2.8 million eggs spawned. In the absence of fishing, a 30% increase would be

expected from a survivorship of 1.84×10^{-3} , or 1 survivor per 53,000 eggs. Population stability is achieved with a survivorship of 6.51×10^{-6} to the age of one year, or 1 survivor per 307,000 eggs. The instantaneous mortality rate for increase, stability, decrease is 10.91, 11.94, or 13.83 on an annual basis, or 0.030, 0.033, or 0.038 on a daily basis.

Neither of the fecundity rates in table 7 could, with values now perceived as reasonable, cause the rates of increase and decline tested. Of the two fecundity rates, batches of egg spawned per year has somewhat more impact than number of eggs per batch. To achieve the declines observed, the eggs per gram of female would have to drop to 39 from 257 or increase to 725 as a secular change. Fecundities approximating this range have been observed for single females. The number of egg batches per year would have to decline to 3.5 or increase to 65 to cause these extreme changes in sardine population growth rate. There might be only 3.5 spawnings per year if the fishery had removed all of the older spawners, but we are refraining from examining multiple effects in the Leslie model until the parameters are given stochastic ranges and the matrix becomes probabilistic rather than deterministic.

Lefkovich Matrix

The instantaneous mortality rates, which yield a 30% decline (table 7B), look reasonable for the egg, yolk-sac, and early larva stages. The static rate is a daily exponential instantaneous rate -0.3 , -0.3 , and -0.14 for the first three stages, and the 30% decline equivalents are -0.887 for eggs, -0.7401 for yolk-sac larvae, and -0.2999 for early larvae. Rate changes of this magnitude for individual stages are probably measurable at sea with existing techniques. Field estimates of instantaneous mortality rates for late larvae through pre-recruits would require equipment that has not yet been designed, and sampling intensity far greater than that now accomplished. With current approaches, the changes in mortality rate in table 7 would probably be undetectable. Similarly, if smaller-parameter changes were distributed among stages, rather than isolated by stage as they are in this simulation, the changes might not be detectable from current field sampling practices.

An effective change in duration of the earlier stages would require protracted periods of extremely warm or cold water to explain secular changes in population growth rates. Temperature's effect on age or size of sardines at first maturity (by analogy to anchovy; Methot 1989) could be an important influence on population growth rate. De-

creasing population caused by slow growth of late larvae, juveniles, and pre-recruits would be easily detectable by otolith daily growth analysis. Secular increases caused by rapid growth would require sustained growth rates of .5 mm per day or more in the late larvae and 1 mm per day or more in juveniles and pre-recruits to be effective (tables 5 and 7B). The more subtle the effect to be measured, the more expense would be incurred; thus sampling costs and required precision would have to be examined from an economic standpoint. Lenarz (1971) showed that recruitment predictions (and assessments) would not have to be very precise to improve the quality of management for sustained economic yield.

DISCUSSION

The primary finding of this study is that a year-class (Leslie 1945) parameterization of critical population growth rates is not likely to reveal important changes in reproductive success of sardines. Although a stage-based (Lefkovich 1965) approach requires much ancillary information, some of the earlier stages could provide useful limits on projections of recruitment as well as the usual stock assessment. Another finding is that the rate of increase in the standing crop of eggs cannot be explained by the fishing moratorium alone. We do not have enough information to decide which other factors may have contributed to the current regional increase of sardine eggs; the sustained increase for nearly two decades is as high as any sustained increase measured for sardine stocks, and higher than most.

Is the current increase due to migration of sardine stocks from other habitats to the southern California area?

With present data, we cannot rule out migration of other elements of the sardine species into this area. If the present stock is from a diminished "northern" stock, it probably arose from the remnants ("founders") of a breeding population of less than 2,000 tons. If the present stock arises from a similarly small group migrating into the area, that population too would arise from "founders," and the distinction may be detected genetically. If there is a constant interchange with other populations, the growth in spawning rates may merely represent added migration rates from a larger stock.

How does the increase of spawning off southern California compare to the increase off Japan?

The rate of increase of eggs per unit area is remarkably close to that off the Pacific coast of Japan; any difference could well be negligible.

Is the increase due merely to the fishing moratorium?

The rate of increase in egg abundance, if due entirely to adult biomass and not to increased spawning rates, is too rapid to be explained by the moratorium alone.

Has the increase been caused by a decline in natural predators?

The rate of increase of the sardine population may have been augmented by the decline of anchovy and mackerel in the same area. These species can prey on early stages of sardines. Bird and mammal biomass, and presumably the consumption of juveniles and adults, have increased, however.

Have other population parameters changed?

Warming would tend to decrease mortality of eggs and yolk-sac larvae, in the absence of other effects, by shortening the most vulnerable stages. Warming may accelerate sardine maturation, as it is thought to do for anchovy (Methot 1989). Not enough is known to speculate about how the other stages might be affected by the interactions among temperature-specific growth rate, the lower plankton volumes associated with warm water, and the introduction of exotic tropical predators associated with warming.

Can normal fluctuations in recruitment rates be detected in time to improve fisheries management?

From examining the life table of sardine, one would expect that the possibility of extremely large recruitment successes could be detected in advance, but not assured, by high egg production and high survival of eggs, yolk-sac larvae, and early larvae. The same has been found likely for anchovy (Smith 1985) and hake (Hollowed, this volume). For sardine, this information would be available nearly two years before recruitment to the fishery. Thus it is more likely to be useful than similar information for anchovy, which recruits at an earlier age. The advance warning would be somewhat longer for hake.

The late larvae and juvenile stages of anchovy, sardine, and hake are not well enough known to yield useful information on abundance, and quantitative sampling of these stages is not now practical. Information on growth rates would be very useful for all stages, since there is an interaction between size and mortality. If *growth and survival* rates were known for sardine eggs and larvae, and *only growth* rates were known for late larvae or early juveniles, then recruitment could probably be categorized as "near," "below," or "above" replacement, from existing sea-survey techniques.

Another feature of sardine recruitment is that on the scale of a few years and a few decades, the recruitment in a given year or decade is likely to be similar in sign to the immediately preceding year or decade (Murphy 1966; Lenarz 1971; Smith and Moser 1988); this should yield particularly useful information for stock management following documented recruitment failures even at higher stock sizes.

Can critical changes in the recruitment rate be predicted from observations of the sardine's physical and biological environment?

It does not seem likely that the necessary lists of age structure, fecundity rates, mortality rates, and growth rates at all seasons of the year will be known to sufficient accuracy (Lo 1986). Also, the biological and physical influences of environment have not been sufficiently well related to these population rates to be predicted by simple environmental indices: this is why environmental indices fail to meet the test of time (Lasker and MacCall 1983). For example, offshore transport of sardine larvae at the height of upwelling might be counteracted to some degree by increased food supply for the juveniles. We do not know which areas of the ocean are occupied by juvenile sardines (and juveniles of most of other species); therefore the physical and biological characterization of their immediate environment is not currently possible. Existing knowledge does not warrant consideration of single factors in the life table, let alone interaction among these factors. Current knowledge on the status of other pelagic fish stocks could help interpret the recruitment success of a sardine population (Butler 1991).

CONCLUSION

It should not be inferred from our emphasis on decadal-scale change that we believe that shorter-scale changes in recruitment are unimportant: it may well be that for fisheries management the interannual scale of recruitment is more important than the longer scale. Unfortunately, matrix methods and even life tables are less appropriate at the shorter time scales.

In general, we have found that the rapid apparent growth rate of the stocks of Pacific sardine off southern California is not likely to have resulted from the fishery moratorium alone: other parameters of survival and reproduction are probably acting in concert with the lowered fishing mortality rate if the population conforms to the models used in this study. It is possible that information on egg production and survival in the earliest life stages, together with growth rates of the later life stages before

recruitment could contribute to better fishery management.

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LEOPARD SHARK

History of the Fishery

The leopard shark (*Triakis semifasciata*) is valued as both a food and game fish in California; it is not uncommon in fresh fish markets and has a firm, mild-tasting flesh. The distinctive markings and hardiness of this fish also make it desirable for aquarium displays.

The scope of the fisheries for leopard shark is difficult to estimate for two reasons: an unknown portion of the commercial catch may be landed under the general category "shark, unspecified"; and statistics on leopard sharks caught by recreational anglers have been inadequate until the beginning of the last decade.

Total commercial landings for California reported under the "leopard shark" category have ranged from 9,270 pounds in 1958 to 101,309 pounds in 1983. The value to fishermen averaged around \$37,000 per year in the 1980's. These landings, while not extensive, have increased in the south and decreased in the north over the past decade. Landings in southern California began increasing in 1981, and in 1985 surpassed landings in northern California for the first time since the collection of statistics began in the 1940's. Legislative curtailment of inshore gillnetting in the San Francisco/Monterey Bay area probably contributed to much of the decline in northern California landings after 1986.

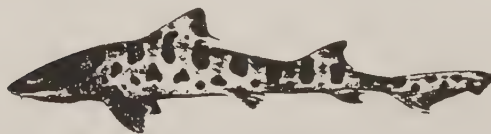
Judging from estimates made since 1980 by the National Marine Fisheries Service (NMFS) Marine Recreational Fisheries Statistics Survey, the recreational leopard shark catch appears to be greater, although these estimates are subject to large sampling variability. According to the survey, sport landings in California between 1980 and 1987 averaged over 270,000 pounds per year and were estimated at 719,608 pounds in 1987.

The importance of recreational anglers as users of the resource in central California was confirmed by analysis of recovery patterns of 948 tagged fish released in the San Francisco Bay area in 1979 by the NMFS. About 82 percent of the 108 recoveries were returned by sport anglers, while only 12 percent were returned by commercial fishermen. Of the recrea-

tionally caught returns, 54.5 percent came from skiff/private boat anglers, 40.9 percent came from shore anglers, and only 4.5 percent came from partyboat anglers. Leopard sharks are commonly taken from piers and jetties, and are known to congregate around the warm water outfalls of power plants.

A variety of fishing methods and gear types are used in the fisheries for leopard sharks: angling with baited hooks, spearfishing by divers, gillnetting along the coast, and some commercial longlining. Recreational spearing reportedly occurs in Humboldt Bay in shallow water. Gillnet catches will probably continue to decline with increasing legislation restricting use of these nets in coastal waters. Some leopard sharks are also taken incidentally in ocean bottom trawl catches.

Because of its slow growth rate, late sexual maturity, low fecundity, and easy accessibility to fishermen, this species is considered susceptible to fishing pressure. Fishing mortality rates and life history parameters indicate that with the current amount of fishing pressure, some measure of protection would be necessary to assure population replenishment.



Leopard shark, *Triakis semifasciata*.

Status of Biological Knowledge

The leopard shark, also known as "tiger shark" and "cat shark," ranges from Mazatlan, Mexico, into the northern Gulf of California, and north to Oregon. Abundant in cool to warm temperate zones, it is most common in shallow water from the intertidal down to 15 feet and less so in deeper water down to 300 feet. This species seems to favor enclosed muddy bays and sloughs, especially in northern California, although it is not unusual to find it along the open coast and around islands off southern California, where it frequents kelp beds and sandy bottoms near rocky reefs.

The population structure throughout its range is not clearly understood, but is thought to consist of regional stocks among which there is relatively little exchange. Nevertheless, tagging studies in central California have shown that there is some mixing between stocks in San Francisco Bay and Elkhorn Slough in Monterey County. There is no information on exchange among other regional stocks, but such exchange is presumed to be limited.

By examining calcified growth zones in vertebral centra, age and growth of leopard sharks from central California have been determined. Growth rate is generally slow (averaging less than one inch per year), with considerable individual variation. The maximum recorded and verified length is about six feet; however, most adults are smaller than that. The maximum age is presumed to be around 30 years; the oldest ages that have been determined by reading calcified rings on vertebrae, are 24 years for a 53-inch male, and 20 years for a 51-inch female. The

largest female aged so far (a 55-inch specimen) was estimated at 19 years. Size at birth is about eight to 10 inches in total length.

The live-bearing female leopard shark produces from seven to 36 offspring in an annual reproductive cycle. Males mature at seven years, and females at 10 years, when fish reach lengths between 40 and 42 inches total length. The gestation period is estimated at 10-12 months. Birth apparently takes place in the spring from March through July. The only known eye-witness account of leopard sharks giving birth in the wild is that of a fisherman who observed pupping activity at Catalina Island in southern California in the 1940's. Dozens of large females, with backs and dorsal fins breaking the surface of the water over a shallow mudflat in Catalina Harbor, were observed releasing their pups in the three to four-foot deep water; some of the pups were seen milling around in water only about a foot deep.

This shark is an opportunistic benthic feeder. Invertebrates taken include crabs, ghost shrimp, clam siphons and sometimes whole clam bodies, polychaete worms, fat innkeeper worms, and octopi. Fishes in the diet include herring, anchovy, topsmelt, croakers, surfperches, gobies, rockfishes, midshipman, flatfishes, and small elasmobranchs such as smoothhounds, guitarfish, and bat ray. Leopard sharks seasonally consume the eggs of herring, topsmelt, jacksmelt, and midshipman.

Predators of the leopard shark are not known, but young or smaller individuals may be preyed upon by larger sharks such as the sevengill and sixgill sharks, which are known to enter bays. The phenomenon of young sharks being preyed on by larger sharks is not uncommon.

These strong swimming, nomadic sharks often occur in schools, sometimes with smoothhounds, which also belong to the houndshark family. Numbers of animals may suddenly appear in an area, then move on. Although generally timid and wary of divers, there is one record of an attack on a skin diver in 1955 in California. Pectoral fin nipping of smaller individuals by larger ones has been observed in fish held in captivity. Evidence attests to the hardiness of these fish, both in their ability to thrive in captivity, and in their capacity to recover from the trauma of hooking injuries.

Migrations of this species have been studied in central California. Results of the San Francisco Bay tagging project revealed that at least 10 percent of the resident population moves out of the bay into the ocean during fall and winter. A fish tagged in San Francisco Bay was recaptured in Elkhorn Slough and vice versa, indicating some exchange between these stocks.

Status of Population

The size of the California leopard shark population has not been estimated, and the only information on relative changes in stock abundance is that which can be inferred from catch statistics. There is evidence, however, that fluctuation in catches may not be a reliable indicator of changes in stock abundance, as environmental conditions may also affect patterns of availability or vulnerability of leopard sharks to capture. Increased commercial and recreational catches have been observed in the San Francisco area in heavy delta outflow years,

increases that tagging results indicate do not appear related to immigration of sharks from other areas.

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Abstract.—Pelagic armorhead *Pseudopentaceros wheeleri* are the target of a directed trawl fishery on many of the southern Emperor–northern Hawaiian Ridge seamounts. The population dynamics of armorhead for the period 1970–90 were reconstructed for Southeast Hancock seamount, the southernmost of the seamounts commercially fished, by using commercial catch-and-effort statistics, various biological measurements, and research stock-survey data. The population declined almost continuously from a 1972 high of 5500 metric tons (t) to a 1989 low of 25t. In addition to the intense fishery, this decline was due partly to the sporadic pattern of armorhead recruitment. Natural mortality rate was estimated as 0.54/year; however, females had a higher mortality rate than males.

Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on Southeast Hancock Seamount

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Pelagic armorhead *Pseudopentaceros wheeleri* have an unusual life history that includes two distinct postlarval phases: a pelagic juvenile phase, and a demersal adult phase. During the first 1.5–2.5 years of their lives (Uchiyama and Sampaga 1990), juvenile armorhead inhabit the epipelagic zone over a broad area of the northeast Pacific, where they acquire large fat reserves before migrating westward to the southern Emperor–northern Hawaiian Ridge (SE–NHR) seamounts (Boehlert and Sasaki 1988, Humphreys et al. 1989). After arriving at the seamounts, armorhead mature and assume demersal habits. Because of the rigors of spawning or the inability to obtain sufficient prey (Seki and Somerton, In prep.), adult armorhead subsequently lose weight to such an extent that they eventually become emaciated and moribund (Humphreys et al. 1989).

Armorhead form dense nighttime aggregations over the relatively flat summits of the SE–NHR seamounts. Soon after these aggregations were discovered in 1967, they were subjected to intense fishing effort first by Soviet trawlers (Komrakov 1970) and 2 years later by Japanese trawlers (Sasaki 1986). The combined annual catch of armorhead rapidly increased and reached a high of

164,000 metric tons (t) in 1973 (Borets 1975, Takahashi and Sasaki 1977) before plummeting to 875t in 1978. This decline in catch was evidently due to a decline in armorhead abundance, because the Japanese catch-per-unit-effort (CPUE) showed a corresponding drop from a high of 54.0t/hr in 1972 to 0.4t/hr in 1978 (Sasaki 1986).

Although never a participant in this fishery, the United States became involved in 1976 when implementation of the Magnuson Fishery Conservation and Management Act extended its exclusive economic zone (EEZ) to include the Hancock Seamounts, the southernmost of the SE–NHR seamounts supporting the armorhead fishery. Although Soviet trawlers ceased operations on the Hancock seamounts after the jurisdictional change, Japanese trawlers continued to fish but were subject to an annual harvest quota and were required to carry U.S. observers who monitored the catch. Regardless of these management efforts, catch rates continued to decline and the Japanese discontinued fishing on the Hancock Seamounts in 1984. In response to the apparent stressed condition of the armorhead population, the National Marine Fisheries Service (NMFS) in 1985 initiated a stock

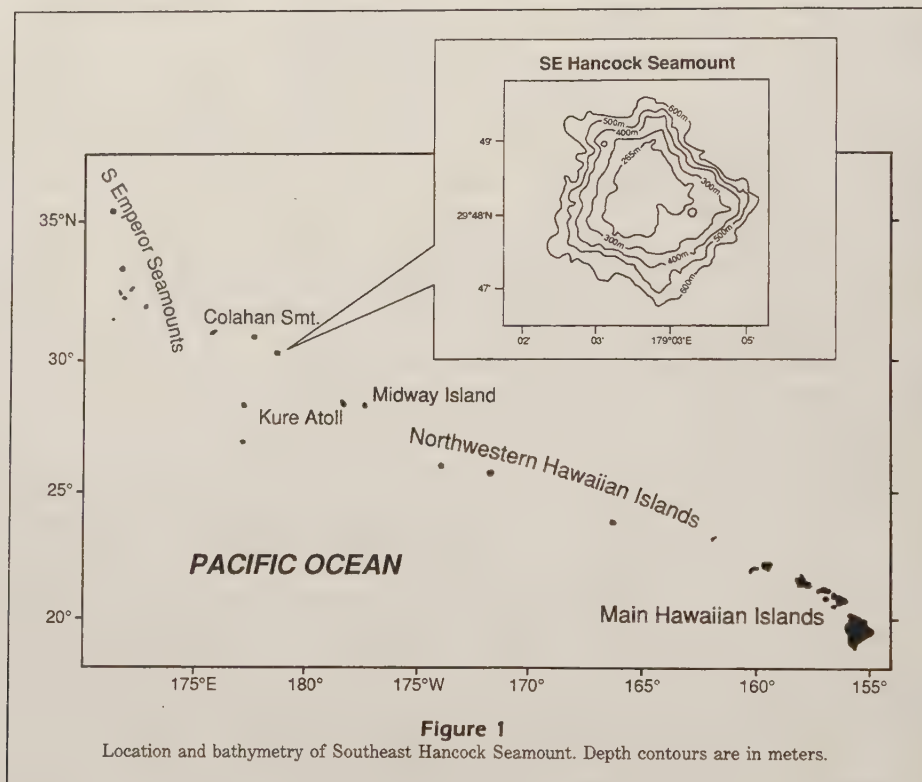


Figure 1
Location and bathymetry of Southeast Hancock Seamount. Depth contours are in meters.

assessment program to monitor armorhead abundance, and in 1986 enacted a 6-yr moratorium prohibiting trawl fishing on the Hancock Seamounts.

The population dynamics of pelagic armorhead have been previously examined (Borets 1975, Wetherall and Yong 1986); however, the results of these studies are questionable because they were based on either Soviet or Japanese catch-and-effort statistics but not both. The present paper attempts to rectify the problem of incomplete data by focusing solely on the stock of armorhead inhabiting the Southeast (SE) Hancock Seamount, where catch-and-effort statistics were supplemented with various biological and vessel performance data after the initiation of the U.S. observer program in 1977 and were completely replaced by research stock-survey data when the commercial fishery ended. With these additional data, it is possible to obtain absolute estimates of armorhead abundance, rather than relative estimates, and to extend the time-series of such estimates beyond the termination of the commercial fishery. In addition to developing a continuous record of armorhead abundance since the initiation of the

fishery, this paper also includes estimates of the natural mortality rate and annual recruitment of pelagic juveniles to the seamounts.

Materials and methods

SE Hancock Seamount

The Hancock seamounts consist of two peaks, Northwest (NW) and SE Hancock Seamount, separated by 61 km and situated on the NHR ~293 km northwest of Kure Atoll, the northernmost of the Hawaiian Islands, and ~287 km southeast of Colahan Seamount, the closest seamount supporting an armorhead fishery (Fig. 1). The SE Hancock Seamount is shaped somewhat like a truncated cone with a relatively flat, smooth summit and steep, rugged flanks (Fig. 1). This topography, combined with the tendency of armorhead to nocturnally migrate from the flanks to the summit (Humphreys and Tagami 1986), constrained the commercial trawl fishery to operate primarily on the summit (<300 m) at night (Sasaki 1986).

Types of data and preliminary analysis

Since the types of data available for describing the population dynamics of armorhead have changed with time, it is convenient to separate the entire 1970–90 interval into three periods: (1) 1985–90, when NMFS stock surveys were conducted but no commercial fishing occurred; (2) 1978–84, when regulated Japanese fishing occurred with U.S. observers aboard the vessels; and (3) 1970–77, when unregulated Japanese and Soviet fishing occurred.

Period 1 In the period 1985–90, NMFS conducted 10 armorhead stock-survey cruises to SE Hancock Seamount. Although bottom trawls were occasionally used, the primary sampling gear was a bottom longline. Unlike trawls, longlines could be used on the steep flanks of the seamount and allow sampling of the entire population. Longlines consisted of 30 rigid poles (droppers), each with 5 equally-spaced hooks on short leaders, attached at 18 m intervals along a 600 m groundline (Shiota 1987). On all cruises, longlines were set perpendicular to the depth contours to maximize the depth range sampled and were fished with the same bait (squid), hook size (no. 20 circle), soak time (1 hr), and fishing period (0800–1830 hr) to maintain constant catchability. Starting in 1986, however, catchability changed slightly when hook timers (small timing devices that are activated when a fish strikes the hook; Somerton et al. 1989) were installed on the leaders. To estimate the effect of timers on armorhead catchability, a comparison experiment was conducted in 1990 in which droppers were alternated with and without timers along the longline. A correction coefficient accounting for the effect of timers on catchability was then estimated as the ratio of the armorhead catches for droppers with timers to those without timers (this ratio was 0.77).

Since preliminary information indicated that armorhead density varied with depth on the seamount, stock surveys were based on a depth-stratified sampling design. Fishing depths were estimated by recording a depth profile of the bottom as the longline was set, then partitioning the measured distance between the terminal anchors into 30 equal intervals (the number of droppers). To help correct for possible differences between fathometer depths and actual fishing depths due to horizontal drift while the longline sank, maximum depth recorders were placed on both anchors and at the midpoint of all longline sets. Recorded maximum depths were used instead of fathometer depths to determine where the anchors and midpoint lay along each depth profile.

When longlines were retrieved, the species identity of each captured fish was recorded along with the number of the hook on which it was caught. All fish

from each 5-dropper segment of the longline were then placed together into a basket for later collection of the following biological attributes: sex, fork length (FL, mm), and body depth (BD, mm) which is the shortest distance between the bases of the first anal spine and the dorsal fin. In 1985, body weight (W, g) was also measured on some specimens in addition to body depth. Equations predicting BD from W and FL, and predicting W from BD and FL, were calculated from these data by using multiple regression. These equations are:

Females ($n = 436$)

$$BD = 86.69 - 0.19FL + 0.10W \quad (R^2 = 0.91)$$

$$W = -936.25 + 9.06BD + 2.49FL \quad (R^2 = 0.90)$$

Males ($n = 476$)

$$BD = 75.55 - 0.18FL + 0.10W \quad (R^2 = 0.85)$$

$$W = -934.02 + 7.52BD + 2.82FL \quad (R^2 = 0.87)$$

Although the depth distribution of armorhead on the longline could be determined unambiguously with the sampling procedure used, this was not true for the depth distribution of any of the measured or derived biological attributes, because the catch from each 5-dropper segment was aggregated before the attributes were measured. As a means of approximating such depth distributions, the biological attributes of individual fish within each segment group were randomly assigned to the capture depths within the segment.

The relative abundance of armorhead during each stock-assessment cruise was expressed as the mean catch in numbers per hook ($\bar{U}$) estimated as a weighted average over four depth strata (<265, 265–300, 301–400, 401–500 m). Algebraically, ($\bar{U}$) is

$$\bar{U} = \frac{\sum_{i=1}^4 U_i A_i}{\sum_{i=1}^4 A_i}, \quad (1)$$

where U_i is the catch per hook, and A_i is the bottom area in depth stratum i . Values of U_i were corrected for the influence of hook timers, and values of A_i were estimated as planar areas between the strata depth boundaries measured on a bathymetric map of the SE Hancock Seamount (Fig. 1).

Since armorhead begin to lose weight after arriving at the seamounts, we examined an index of relative fatness (FI), defined as body depth divided by fork length, as an index of post-recruitment age. Frequency distributions of FI were calculated as weighted averages, where the weighting factors were proportional to the estimated abundance of armorhead in each depth stratum. Algebraically, this is expressed as

$$\bar{N}_j = \frac{\sum_{i=1}^4 N_{ij} A_i U_i}{\sum_{i=1}^4 A_i U_i}, \quad (2)$$

where N_{ij} is the number of fish in FI category j and depth stratum i .

The frequency distributions of FI usually display two or three distinct modes which are similar in appearance to the modes often present in length-frequency distributions of temperate fishes. Since armorhead recruitment to the seamounts is seasonal (Boehlert and Sasaki 1988), these modes were assumed to represent annual cohorts of fish. To estimate the proportion of the population contributed by each cohort (P_k) and the mean and variance of its FI distribution, the FI distributions were separated into their component distributions by fitting a distribution mixture model using a procedure developed for length-frequency data (Macdonald and Pitcher 1979).

Several of the year-class modes in the FI distributions were so distinct that they could be followed through the time-series in an orderly progression from when they were fat (high FI) to when they were lean (low FI). This feature of the FI distributions was used in two ways. First, the rate at which armorhead decrease in fatness was estimated by following the particularly strong year-class recruiting to the seamount in 1986. Mean FI of this cohort (μ_k) on each cruise was regressed against the time (in months), and the time squared, since the cohort was considered fully recruited to the seamount. Linearity of the relationship was determined by the significance of the coefficient of the squared term.

Second, the instantaneous natural mortality rate (M) of armorhead was estimated by following two cohorts, one composed of armorhead recruiting to the seamount in 1986 and the other composed of all armorhead present on the seamount during the first cruise in 1985. Relative abundance of each cohort at each time (t) was first estimated as the product of the catch-per-hook and the proportion of the population within the appropriate cohort on each cruise; that is, $P_{k,t} \bar{U}_t$. Instantaneous natural mortality rate was then estimated by regressing the natural logarithm of relative abundance against the time (in months) since the cohort was considered fully recruited. Analysis of covariance (ANCOVA) was used to test whether the slopes of the regression lines (i.e., the estimated values of M) differed between cohorts. A best estimate of M was computed as the average of the estimates for the two cohorts weighted by the inverses of their variances. Additionally, M was estimated for each sex separately, considering only the 1986 cohort. ANCOVA was again used to test whether

the estimated values of M differed between sexes. These and all subsequent applications of ANCOVA herein will first test a model with one slope and two intercepts against a model with two slopes and two intercepts. If such a test is not significant, then a model with one slope and one intercept is tested against a model with one slope and two intercepts.

Period 2 In the period 1978–84, Japanese trawlers conducted 10 fishing trips to SE Hancock Seamount. For all trips, U.S. observers recorded the weight of armorhead caught and the duration of each trawl-haul. In addition, fork length and body weight were recorded for a random sample of armorhead drawn from each haul.

The biomass of armorhead at the start of each fishing trip was estimated by using the Leslie method (Leslie and Davis 1939) in which the change in CPUE over time is related to the cumulative catch removed. Algebraically, this is expressed as

$$U_d = B_0 q - q K_d, \quad (3)$$

where U_d is the daily average catch (in kg) of armorhead per hour of fishing on day d , K_d is the cumulative catch of armorhead up to the beginning of day d , q is the catchability coefficient, and B_0 is the initial biomass. Two parameters (q , B_0) were estimated by regressing U_d on K_d ; variance of B_0 was estimated using the equation from Polovina (1986). Mean catchability, $\bar{q}_j$, and its variance were calculated from the per-trip estimates.

Frequency distributions of FI were computed the same as for Period 1, except that body depths were not measured but were estimated from body weights and fork lengths using the regression equation previously described. Since the distributions showed apparent cohort modes similar to those observed during Period 1, the mean and variance of the FI distribution for each cohort and the proportional contribution of the cohort to the population were again estimated with a distribution mixture model. The rate at which FI decreased with time was estimated by regressing the mean FI of the cohort recruiting in 1980 against the time (in months), since the cohort was considered fully recruited.

Period 3 In the period 1970–77, Japanese trawlers fished Hancock Seamounts for at least 1 month in every year; however, data from NW and SE Hancock Seamounts could not be separated. Soviet trawlers also likely fished the Hancock Seamounts over this period, but the available Soviet data (Borets 1975) were aggregated over all seamounts and were not useful for determining the stock dynamics on the Hancock Seamounts.

Relative abundance of armorhead was therefore based solely on Japanese data and was calculated as the reported monthly catch divided by the fishing effort (in hr). Annual mean catch-per-hour ($\bar{U}_t$) and its variance were calculated from the unweighted monthly means. FI could not be calculated during this period due to insufficient data.

Biomass estimation

Armorhead abundance could be estimated in absolute terms as biomass only in Period 2. In the other periods, abundance was estimable in relative terms as CPUE. To allow estimation of biomass from CPUE in Periods 1 and 3 and to allow the merging of all three periods into one continuous time-series, several parameters were required that could be estimated only with data from Period 2. For this reason, we will start by describing the biomass estimation procedures for Period 2.

Period 2 The initial biomass estimates obtained for Period 2 (i.e., Leslie estimates of initial biomass in each year, $B_{0,t}$) may not include the total biomass of armorhead on the SE Hancock Seamount. Instead, the initial estimates may include only the biomass of the fishable stock or that portion of the stock occurring on the summit at night and therefore vulnerable to trawls. The question of whether $B_{0,t}$ includes the total population was addressed by testing the equality of two different estimators of annual recruitment to the seamount. The first (R_1) was calculated as the difference between the estimated biomass in 1 year minus the expected biomass surviving from the previous year. Assuming that the catch was taken in a brief interval at the start of the year, this relationship can be expressed as

$$R_{1,t+1} = B_{0,t+1} - (B_{0,t} - C_t) e^{-M}, \quad (4)$$

where $B_{0,t}$ and $B_{0,t+1}$ are the biomass estimates in years t and $t+1$, C_t is the catch in year t , and e^{-M} is the annual survival rate. The second (R_2), is calculated as the proportion of the biomass composed of recently recruited fish:

$$R_{2,t+1} = B_{0,t+1} P_{r,t+1}, \quad (5)$$

where $P_{r,t+1}$ is the proportion of the population composed of the cohort recruiting in year $t+1$. If $B_{0,t}$ estimates include the total biomass, then they will be appropriately scaled to C_t , and R_1 will equal R_2 . But if the $B_{0,t}$ estimates are less than the total biomass, then R_1 will be greater than R_2 . Equality was tested using the statistic

$$Z = \frac{R_1 - R_2}{\sqrt{\text{Var}(R_1 - R_2)}}, \quad (6)$$

where Z was assumed to be distributed as a normal random variable. Estimates of $\text{Var}(R_1 - R_2)$ were computed as described in the Appendix.

The fishable proportion of the stock (P_f) was estimated in two stages. First, total biomass of the 1980 cohort was estimated for each year in 1980–84, when the 1980 cohort represented more than 90% of the total population, by using an age-structured analysis (Megrey 1989) applied to a single cohort. Starting with a known or assumed value of biomass at the beginning of 1985, this analysis sequentially predicts biomass in each preceding year by accounting for catch and natural mortality. If the catch occurs over a short period at the start of the year, total biomass of this cohort in each year ($B^*_{t_0}$) can be expressed as

$$\begin{aligned} B^*_{t_0-1} &= B^*_{t_0} e^M + C_{t_0-1} \\ B^*_{t_0-2} &= B^*_{t_0-1} e^M + C_{t_0-2} \\ &= B^*_{t_0} e^M + C_{t_0-1} e^M + C_{t_0-2} \end{aligned} \quad (7)$$

$$B^*_{t_0-n} = B^*_{t_0} e^{nM} + \sum_{i=1}^n C_{t_0-i} e^{(n-i)M},$$

where $B^*_{t_0}$ is an estimate of total biomass at the start of the last year (t_0) in the time-series (terminal biomass), and C_{t_0-i} is the catch in year t_0-i . Second, the proportion fished in each year ($P_{f,t}$) was then estimated as $B_{0,t}/B^*_{t_0}$, and mean P_f was then estimated as the average of the five annual estimates. This estimate of P_f , however, was not unique because it depended on $B^*_{t_0}$, and $B^*_{t_0}$ was chosen arbitrarily because no independent estimate was available. Therefore, the terminal biomass B^*_{85} (the terminal fishing year was defined as 1985 as a later convenience) was estimated along with P_f . Assuming P_f is a constant, the two parameters were estimated by minimizing the weighted sum of squares of the $P_{f,t}$ with weights equal to the inverse of the variance of each $P_{f,t}$.

Once the estimate of mean P_f had been obtained, corrected estimates of the initial biomass in each year (i.e., corrected Leslie estimates) were estimated as

$$B^*_{0,t} = \frac{B_{0,t}}{P_f}, \quad (8)$$

and the mean annual biomasses were then estimated as

$$B_t^* = \frac{U_t}{q_t P_t}, \quad (9)$$

where U_t and q_t are the mean annual CPUE and catchability. Variance of B_t^* was estimated with methods described in the Appendix.

Period 3 Biomass during Period 3 was estimated from the mean catch-per-hour of Japanese trawlers (U_t) as

$$B_t^* = \frac{U_t}{q_j P_f}, \quad (10)$$

where q_j is the mean catchability of Japanese trawlers estimated for Period 2. Variance of B_t^* was estimated with methods described in the Appendix.

Period 1 Biomass during Period 1 was estimated from longline catch-per-hook (U_t) as

$$B_t^* = \frac{U_t W_t}{q_1}, \quad (11)$$

where W_t is the mean individual weight of armorhead caught during sampling Period t , and q_1 is the catchability of the longlines. Estimation of q_1 required an independent estimate of B_t^* for at least one of the sampling periods, and the estimate chosen was the terminal biomass of the 1980 year-class in 1985. Catchability was thus estimated as

$$q_1 = \frac{U_{85} P_{80} W_{85}}{B_{80,85}^*}, \quad (12)$$

where U_{85} is the catch-per-hook, W_{85} is the mean body weight in 1985, $B_{80,85}^*$ is the terminal biomass of the survivors of the 1980 year-class at the start of 1985, and P_{80} is the proportion of the 1985 population composed of the 1980 year-class survivors. Variances of B_t^* and q_1 were estimated with the methods described in the Appendix.

Spawning and recruitment biomasses

Spawning and recruitment biomasses were estimated for Periods 1 and 2 in which FI information was available. Spawning biomass in each year (S_t) was estimated as:

$$S_{t+1} = \left(B_t^* - \frac{C_t}{2} \right) e^{-\frac{M}{2}} (1 - P_{r,t}), \quad (13)$$

where $P_{r,t}$ is the proportion of B_t^* comprised of newly-recruited fish, and all other terms are as previously defined. This formulation assumes that B_t^* was always estimated on 1 July, the midpoint of both the fishing season and the stock-assessment cruise. Natural mortality between 1 July and 31 December, the assumed peak of spawning (Bilim et al. 1978), was accounted for by the term $e^{-M/2}$, where M is the annual instantaneous natural mortality rate. $P_{r,t}$ was estimated as the proportion of the population (P_k) within the modal group with the largest mean FI, or as zero if no model group had a mean FI > 0.25. $P_{r,t}$ was included in the estimate of spawning biomass because, based on samples collected on the August 1988 stock-assessment cruise (R. Humphreys, NMFS Honolulu Lab., unpubl. data), female armorhead appear to be nonreproductive during the first spawning season after they recruit to the seamounts. Recruitment biomass was estimated as

$$R_t = \left(B_t^* + \frac{C_t}{2} \right) P_{r,t}. \quad (14)$$

This formulation assumes that recruitment occurs from March to May (Boehlert and Sasaki 1988) and is complete by the time B_t^* is estimated. Since young armorhead recruit to the seamounts at approximately 24–30 months of age (Uchiyama and Sampaga 1990), recruitment follows spawning by 3 calendar years. Spawner-recruit relationships were therefore examined using a 3-year lag between spawning and recruitment.

Results and discussion

The armorhead population on SE Hancock Seamount fluctuated tremendously between 1970 and 1990 (Fig. 2) and declined steadily after the population high in 1972, except for small increases occurring in 1980 and 1986. Before the forces producing these changes (i.e., natural mortality, fishing mortality, and recruitment) are examined, the potential biases and the precision of the biomass time-series will be considered.

Biomass estimates

Construction of the time-series of biomass estimates required (1) merging two time-series of CPUE data that were non-overlapping in time and were from distinctly different gear types, and (2) the conversion of a relative measure of abundance (CPUE) into the absolute measure of biomass. Since Japanese trawls and research longlines were never used simultaneously, the time-series could not be merged by simply standardizing the catchability of one gear relative to the other. Fortunately, however, the armorhead popula-

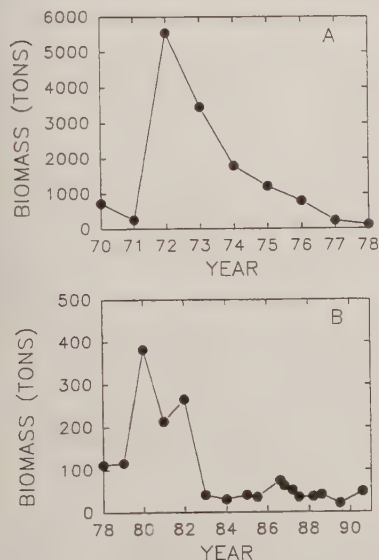


Figure 2

Pelagic armorhead *Pseudopentaceros wheeleri* biomass on Southeast Hancock Seamount during periods of (A) high abundance (1970-78) and (B) low abundance (1979-90). Prior to 1985, when routine stock-assessment surveys were initiated, the biomass estimates are annual means and are shown at the beginning of the year. Starting in 1985, the biomass estimates are for each stock-assessment survey and are shown for the appropriate month.

tion on SE Hancock seamount was sufficiently small and the fishing effort was sufficiently large to allow use of the Leslie method to estimate both the mean catchability of the trawlers (q_j) and the biomass at the initiation of each fishing season ($B_{0,t}$) during the period just prior to replacement of commercial trawling by research longlining. The time-series was merged by using the estimate of q_j and P_f to compute biomass from Japanese trawl CPUE and by using the estimates of $B_{0,t}$ to estimate q_j and thereby compute biomass from longline CPUE. Thus, the Leslie method provided the means to merge the two time-series and to express the resulting time-series in terms of biomass.

Because success of this procedure rests on the successful application of the Leslie

Table 1

Leslie estimates of initial biomass (B_0) and catchability (q) of pelagic armorhead *Pseudopentaceros wheeleri* for each of the Japanese fishing trips during Period 2 (1978-84) on SE Hancock Seamount.

Year	Month	Vessel ID no.	Days fished	Catch (t)	B_0 (t)	q	$P(q=0)$
1978	May	1	11	204	198	0.00197	<0.001
1979	Jun	2	18	68	80	0.00059	<0.005
1980	Aug	3	29	453	551	0.00047	<0.001
1981	Jun	2	5	161	297	0.00101	>0.10
	Aug	3	20	44	55	0.00067	>0.10
1982	May	4	10	180	269	0.00064	0.10
	Jul	2	12	8	17	0.00071	>0.10
1983	Jul	3	19	39	38	0.00066	<0.001

method, any biases in the biomass estimates are likely the result of violations of the underlying assumptions. One of the most important assumptions of the Leslie method is that the change in size of the population is solely due to removals by the fishery. In practice, this requires that the population is closed to immigration and the fishery is sufficiently short and intense so that the effect of natural mortality is negligible. In nearly all cases examined, these requirements were met; that is, fishing usually occurred well after the spring peak in recruitment of pelagic juveniles (Table 1; Boehlert and Sasaki 1988) and the catch was usually obtained in 1 or 2 months and represented a large fraction of the estimated biomass (Table 1). One further indicator of the successful application of the Leslie method is the significance of the slope of the regression, or q . Although the estimates of q obtained using the Leslie method were not always significantly greater than zero, they were remarkably similar among years for each vessel that had fished repeatedly (Table 1). Such similarity was used as justification for using the non-significant estimates in later calculations.

Bias could also result from violation of another assumption of the Leslie method, that the entire population is equally vulnerable to the sampling gear. Such bias was considered likely when initial biomass estimates from Period 2 seemed too small to be consistent with the observed catches. This apparent inconsistency was examined statistically by testing the equality of two estimators of recruitment, one that included catch (R_1 ; Eq. 4), and one that did not (R_2 ; Eq. 5). The bias was confirmed since in 4 of the 5 years examined, R_1 was significantly ($P < 0.05$) greater than R_2 , a condition that could occur only if the biomass estimates were too small.

The most likely explanation for the underestimation of armorhead biomass is that the $B_{0,t}$ estimates do not include the entire population and instead include only the fishable population or the part actually exposed to trawls. This result was surprising because we believed that the population would be sufficiently mixed by the nocturnal vertical migration so that all armorhead would be equally vulnerable even though the trawls were topographically restricted to only a part of the armorhead depth range. Our

finding, however, indicates either that mixing is minimal or that the rate of mixing is relatively low compared with the 2- to 4-week duration of a typical Japanese fishing trip.

Although the bias in $B_{0,t}$ was corrected by estimating the proportion of the stock vulnerable to trawling ($P_f = 0.27$), adequacy of this correction rests on the assumption that P_f does not vary with time. However, P_f may vary with time because the depth distribution of armorhead may vary. For example, the proportion of the population occurring in the shallowest depth stratum (<250 m) averaged 15% over the 10 research cruises, but ranged from 0 to 40%. It is unclear if such variation in the daytime distribution is reflected in the nighttime distribution, because armorhead do not feed at night and therefore cannot be sampled effectively with longlines (M.P. Seki and D.A. Somerton, NMFS Honolulu Lab., unpubl. data). Bias in the biomass estimates could additionally occur if P_f depends on the degree of mixing of deep and shallow fish, because P_f would likely be larger when fishing periods were longer and less intense. Since fishing periods tended to be longer during Period 3 than in Period 2, this would lead to an overestimate of biomass during Period 3.

Precision in the estimates of biomass, which is expressed as the coefficient of variation (CV) to compensate for the large range in biomass, was smallest in Period 1 (Fig. 3), because longline CPUE estimates were more precise than trawl CPUE estimates. Expressed differently, based on the mean CV over the period 1970–84 (excluding 1971 when data were not sufficient to estimate the variance of U_t), the 95% confidence intervals for B_T^* was $\pm 1.70 B_T^*$, which in all years includes zero. Over the period 1985–90, however, the 95% confidence interval was $\pm 0.29 B_T^*$, and never included zero.

Post-recruitment ageing

The estimates of natural mortality rate and annual recruitment required estimates of the age distribution. Although the ages of armorhead can be determined using either daily or annual growth increments on their otoliths (Uchiyama and Sampaga 1990), they are easily obtainable only for individuals in the pelagic phase of their life history, because somatic growth ceases once armorhead recruit to the seamount (Humphreys et al. 1989) and growth increments become so closely spaced that they are exceedingly difficult to count (R. Humphreys, NMFS Honolulu Lab., pers. commun.). Thus, we expressed age on a scale relative to the presumed time of recruitment. Such post-recruitment ages were based on the decrease in FI over time.

Frequency histograms of FI display modes which can be tracked sequentially from one histogram to the next over time as they move from the right (high FI or fat) to the left (low FI or lean). Two examples of this are the

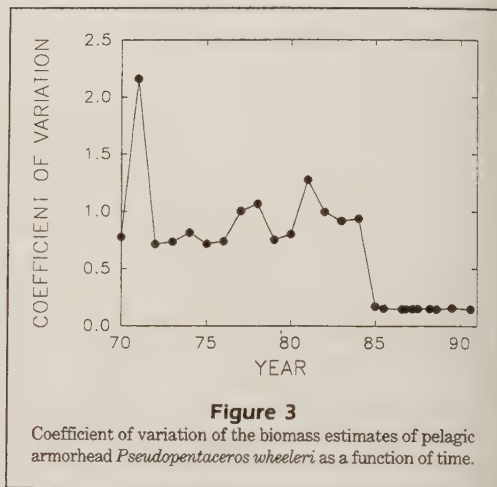


Figure 3

Coefficient of variation of the biomass estimates of pelagic armorhead *Pseudopentaceros wheeleri* as a function of time.

large mode that appeared in 1980 and could be followed until 1984 (Fig. 4A) and the large mode that appeared in 1986 and could be followed until 1990 (Fig. 4B). Since the first appearance of these modes was always associated with an increase in CPUE (Fig. 2B), they were interpreted to represent cohorts of fish that had recruited to the seamount.

To further substantiate our interpretation of the modes, the rate of decrease in FI was examined for consistency both over time and between the two presumed year-classes. Plots of FI versus time appeared to have slight curvature (Fig. 5), but for both the 1980 and 1986 year-classes the curvature was not significant ($P > 0.05$). Changes in FI, therefore, are proportional to changes in post-recruitment age. The rates of decrease in FI of the 1986 (0.00169/mo) and the 1980 (0.00157/mo) year-classes did not differ significantly (ANCOVA, $P > 0.05$). In addition, sexual equality in the rate of decrease in FI was tested for the 1986 year-class alone, and the male rate was not significantly different (ANCOVA, $P > 0.05$) from the female rate. Taken together, these findings indicate that all armorhead decrease in FI at approximately the same rate and that once established by the recruitment of a strong year-class, the coherency of an FI mode should be preserved over time.

Natural mortality

Natural mortality was estimated from the change in the relative abundance of two cohorts over time during a period when no commercial fishing occurred. The first of these cohorts, which consisted

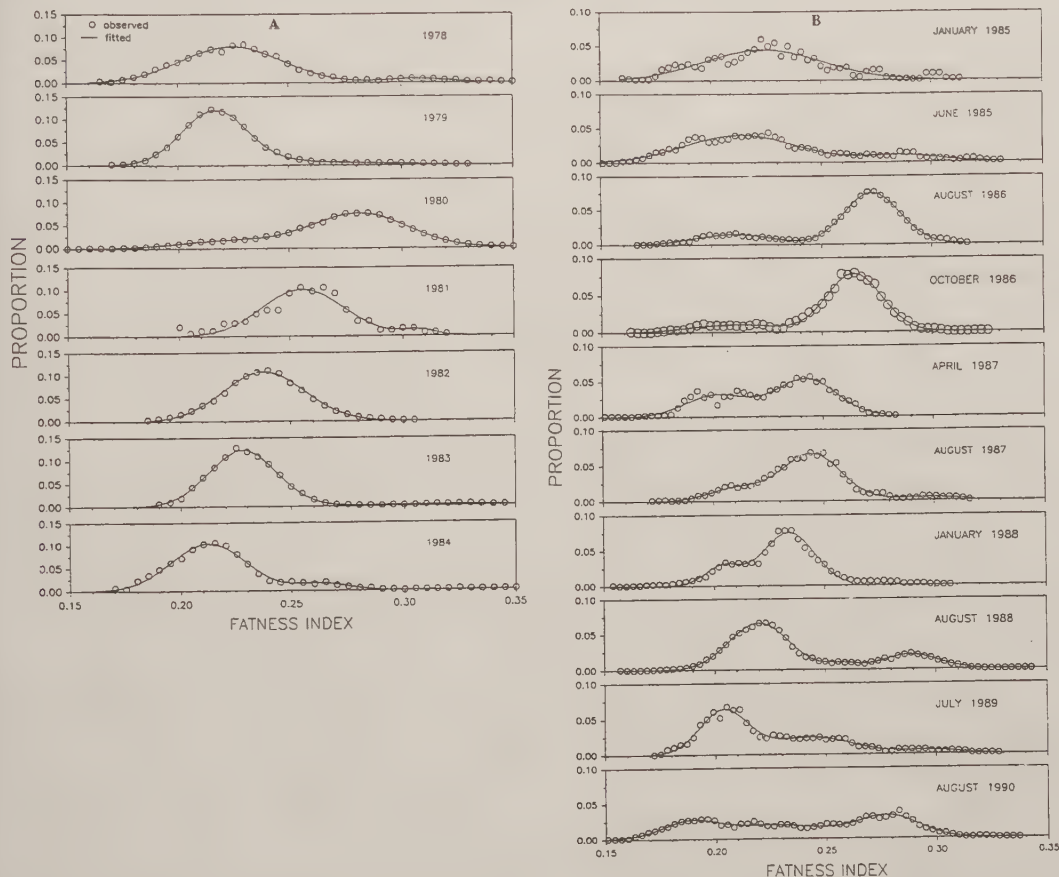


Figure 4

Frequency histograms of fatness index are shown for Japanese commercial catch of pelagic armorhead *Pseudopentaceros wheeleri* in (A) each year during 1978–84 and (B) for each of the research cruises during 1985–90.

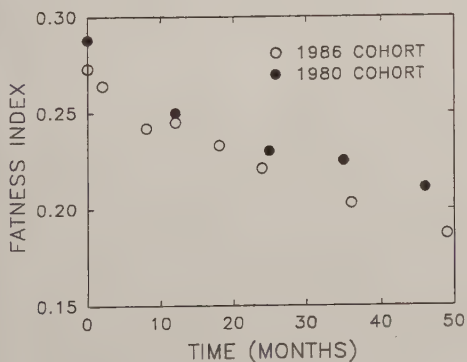


Figure 5

Decrease in fatness index of pelagic armorhead *Pseudopentaceros wheeleri* with time for the 1980 and 1986 year-classes on Southeast Hancock Seamount.

of the extant armorhead population in January 1985, was identifiable for seven consecutive samplings and had an instantaneous natural mortality (M) of 0.054/mo. The second, which consisted of the year-class recruiting in 1986, was identifiable for eight consecutive samplings and had an M of 0.044/mo (Fig. 6). Although the two estimates were significantly different (ANCOVA, $P < 0.05$), the weighted average (0.045/mo or 0.54/yr) was chosen as

the most representative value. For both cohorts, log-relative abundance was clearly a linear function of time, and M is therefore invariant with age (Fig. 6A).

When M was estimated separately for each sex, considering the 1986 cohort alone, the value for males (0.037/mo) was significantly different (ANCOVA, $P < 0.001$) from the value for females (0.045/mo). Furthermore, the intercept of the regression, i.e., the log-relative abundance at the time of recruitment appeared to be smaller for males (4.27) than for females (4.94), but the difference could not be tested because of the strong difference in slopes (Fig. 6B). Taken together, these results indicate that, at least for the 1986 cohort, females recruited to the seamounts in greater abundance than males but subsequently died at a greater rate. It is also possible that the higher mortality rate of females was primarily restricted to the first year of residence on the seamount (Fig. 6B).

Since a sexual difference in mortality seemed inexplicable to us, we examined the possibility that longlines preferentially selected fat females. This was done by examining whether the ratio of females to males, expressed as proportion female, changed with FI similarly for trawls as for longlines. Since the FI values of females and males decrease identically with time, any change in female proportion with FI would indicate either selective sampling or differential mortality, depending on whether one or both gear types showed the change. To test for such changes, female proportion was regressed on FI for various samples. When these regressions were performed on the longline samples, all 10 had a significant ($P < 0.05$) positive slope. When the regressions were performed on the research trawl samples, four of five had a significant positive slope. Thus a sampling bias is unlikely, unless both gears produced a similar bias.

The estimate of natural mortality rate (0.54/yr) is more than twice that reported in Borets (0.25/yr; 1975). His estimate, however, was based on age data that were likely biased for two reasons. First, the age range [i.e., 7 yr, ages 5–12], reported in Borets (1975) appears to be excessive when compared with the range estimated from modal progression through the research FI histograms (4–5 yr). Second, the mean age of the catch between 1968 and 1974 reported in Borets (1975) did not decrease as would be expected in a developing fishery. On the other hand, our estimate of natural mortality rate was less than the rate implied in the studies of Uchida and Tagami (1984), Humphreys et al. (1989), and Uchiyama and Sampaga (1990), which all suggested that armorhead were semelparous and, like Pacific salmon *Oncorhynchus* spp., died soon after spawning.

Fishing mortality

Fishing mortality rate (F) can be estimated only between 1978 and 1983 when the total catch and effort on SE Hancock Seamount are known with reasonable certainty, based on the U.S. observer program. Over this period, F , which was calculated as the estimated value of $q_j \times$ total annual effort, averaged 1.03/yr or roughly twice the natural mortality rate. The mean

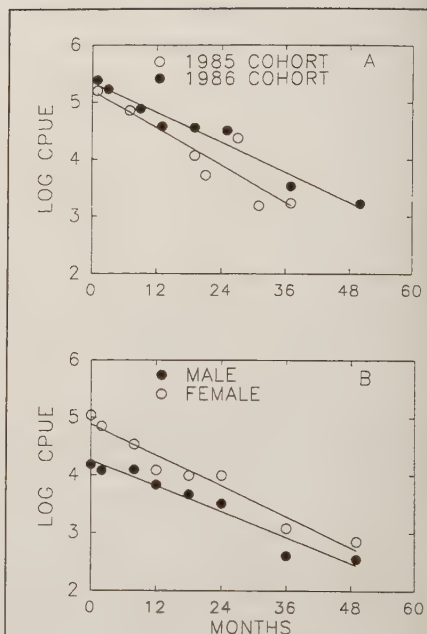


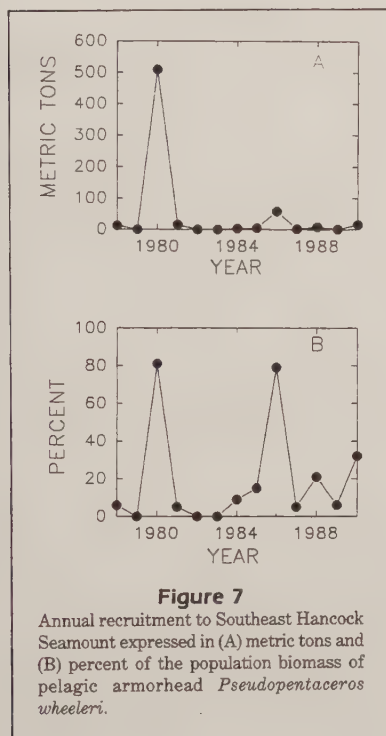
Figure 6

Change in log CPUE of pelagic armorhead *Pseudopentaceros wheeleri* versus time for the (A) cohort composed of the extant population in 1985 and the cohort recruiting in 1986, and (B) for males and females of the 1986 recruiting cohort.

exploitation rate (which was approximated as $(F/Z)(1 - e^{-Z})$ where $Z = F + M$), was ~ 0.50 . Therefore, provided that no recruitment occurred and that fishing effort was continuous throughout the year, then an average of roughly 50% of the population at SE Hancock Seamount was removed annually by the fishery over this period.

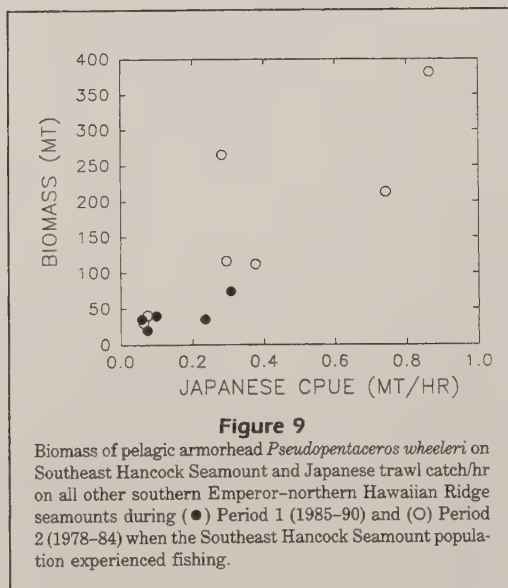
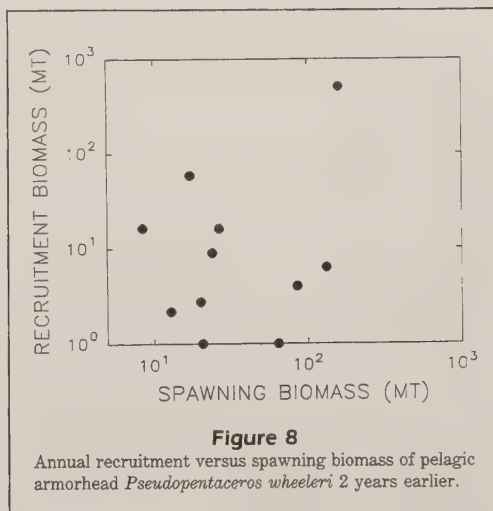
Recruitment

Annual recruitment to SE Hancock Seamount was extremely intermittent between 1978 and 1990. When expressed in metric tons, the 1980 recruitment clearly dominated the entire record (Fig. 7A). However, the total biomass changed considerably over this period, and, when expressed as a percentage of the total biomass, the 1986 recruitment and—to a lesser extent—the 1988 and 1990 recruitments were also relatively important (Fig. 7B). For some



unknown reason, recruitment in the even years tended to be larger than it was in the odd years (Mann-Whitney test, $P = 0.06$).

Prior to 1978, it is difficult to estimate annual recruitment because the data required to calculate FI were not routinely collected. However, an examination of the large increase in abundance in 1972 (Fig. 2A) cannot be avoided. Interpretation of the 1972 increase is troublesome because the evidence for an unusually large recruitment is equivocal. A large recruitment, for example, should have resulted in a large increase in the proportion of the population comprised of fat armorhead as it did in 1980 and 1986 (Fig. 4A,B), yet the proportion of the population categorized as fat during the period of maximum recruitment was smaller in 1972 than it was in 1973 when recruitment did not appear to be exceptionally large (Boehlert and Sasaki 1988). Armorhead measured in 1972, however, were markedly smaller than in any other year (Takahashi and Sasaki 1977, Borets 1975). One proposed explanation for the small size is that the tremendous abundance of armorhead in 1972 resulted in a density-dependent suppression of growth in the pelagic phase (Borets 1977). This might also have reduced the FI of recruits



and thereby masked the FI signature of a large recruitment.

An alternate explanation for the 1972 increase in abundance is that it is an illusion due to a rapid increase in trawl catchability as the newly-developed fishery progressed from an exploratory phase to a production phase (Takahashi and Sasaki 1977, Uchida and Tagami 1984). If, however, the 1972 increase was due simply

to changing catchability, then such an increase should not be evident in the Soviet catch-and-effort data, because the Soviet fishery had developed earlier and was likely beyond its "fishing-up" phase. Soviet data do display an increase from 1971 to 1972 (73–104 million fish/vessel day; Borets 1975), but this is considerably less than that experienced by the Japanese fishery. Thus, it is not entirely clear whether the apparent increase in 1972 was real and due to recruitment or an artifact due to changing catchability.

The dependance of recruitment on spawning biomass was examined by Wetherall and Yong (1986) and found to be essentially nonexistent, at least at the high levels of spawning biomass extant during 1969–77. Recruitment, however, must ultimately be limited by spawning biomass at low population levels; therefore, we reexamined the relationship over the period 1980–90, when the spawning biomass was considerably lower. This was done by plotting, on a log-log scale, the estimated spawning biomass on SE Hancock Seamount against the estimated recruitment 2 years later (Fig. 8). Since a clear relationship is not evident, it is possible that recruitment and spawning biomass are only weakly related even at the low population levels examined. There are, however, at least two other possible reasons why no relationship was found. First, since no apparent genetic difference exists among the armorhead collected at the various seamounts (Borets 1979), recruits to SE Hancock Seamount are likely the progeny of the entire North Pacific population. If the SE Hancock Seamount population does not vary concordantly with the entire North Pacific population, any relationship between recruitment and spawning biomass would be obscured. However, plots of the estimated biomass on SE Hancock Seamount against Japanese CPUE on all SE-NHR seamounts show a strong concordance (Fig. 9). Second, if spawning biomass does exert an influence on recruitment, it may do so only by limiting the maximum level attained. Thus, at higher levels of spawning biomass, higher levels of recruitment are possible—but not assured—because of environmental variability. One interpretation of Figure 8 could therefore be that recruitment did increase with spawning biomass, but at the higher levels of biomass there were several environmentally-poor recruitment years.

Management implications

Since armorhead do not grow after they recruit to the fishery and therefore cannot be growth-overfished, management strategies could be designed solely to achieve some optimum level of spawning stock biomass (SSB). One approach is to define this optimum SSB by

using a spawner-recruit relationship as is done for some species of Pacific salmon (Ricker 1975). Another approach is to define it in terms of a fixed percentage of the equilibrium biomass in the absence of a fishery (Beddington and Cooke 1983). But in either case, the spawning population must include the entire SE-NHR population rather than the small component examined here. In addition, some form of international agreement controlling the armorhead catch will be required before any management measures are effective.

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Appendix

Variances of several of the estimators described in Materials and Methods were approximated by using the Delta method (Seber 1973) and assuming all covariance terms were negligible. Variance of $(R_1 - R_2)$ was estimated as

$$\text{Var}(R_1 - R_2) = (P_{r,t+1} - 1)^2 \text{Var}(B_{0,t+1}) + (B_{0,t+1})^2 \text{Var}(P_{r,t+1}) + e^{-2M} [\text{Var}(B_{0,t}) + \text{Var}(C_t) + (B_{0,t} - C_t)^2 \text{Var}(M)], \quad (15)$$

where all variables are defined in text Equations 5 and 6. Variances of $B_{0,t}$ and $B_{0,t+1}$ were computed by using the method in Polovina (1986). Variance of C_t was assumed to be negligible because catch was measured by U.S. observers. Variance of M was estimated as the variance of the slope of the regression of log-relative abundance on postrecruitment age (in years). Variance of $P_{r,t+1}$ was estimated with a bootstrap method (Efron and Gong 1983). Bootstrap estimates were obtained from trawl samples of armorhead biological data by iteratively repeating the following steps: (1) A subsample of n fish from each sample was randomly chosen with replacement, where n is equal to the size of the original sample; (2) an FI frequency distribution was constructed from the subsample; (3) $P_{r,t+1}$ was estimated by fitting the distribution mixture model to the FI frequency distributions. In all cases, variance of $P_{r,t+1}$ was calculated as the variance among 100 bootstrap estimates.

Variance of B_t^* during Period 2 was as

$$\text{Var}(B_t^*) = \left[\frac{1}{q_t P_f} \right]^2 \text{Var}(U_t) + \left[\frac{U_t P_f}{(q_t P_f)^2} \right]^2 \text{Var}(q_t) + \left[\frac{U_t q_t}{(q_t P_f)^2} \right]^2 \text{Var}(P_f) \quad (16)$$

where all variables are defined in Equation (9). Variance of U_t was estimated as the variance among the daily U within each year. Variance of q_t was estimated as the variance of the slope of the Leslie model. When more than one vessel fished in each year, however, variance of q_t was the average of the individual variance estimates weighted by catch.

Variance of P_f was estimated by using a Monte Carlo model. Each iteration of the model consisted of generating a random value of $B_{0,t}$ for each year and a value of M , assuming all were normally distributed with means and variances equal to the original estimated values. With these generated values, B_t^* was estimated for each year with Equation (9) and $P_{f,t}$ was estimated as $B_{0,t}/B_t^*$. Mean estimates of P_f and $B_{80,85}^*$ (B_{t0}^* in Eq. 7), were obtained by using the iterative procedure to minimize the weighted sum of squares of the $P_{f,t}$ estimates. In all cases variances of P_f and $B_{80,85}^*$ were estimated from 100 iterations of the Monte Carlo model.

Variance of B_t^* during Period 3 was estimated using Equation (16) but with q_t replaced by q_j . Variance of U_t was estimated as the variance among the monthly means. Variance of q_j was estimated as the variance among the q estimates in Table 1. Variance of P_f is the same as for Period 2.

Variance of B_t^* during Period 1 was estimated as

$$\text{Var}(B_t^*) = \left[\frac{W_t}{q_1} \right]^2 \text{Var}(U_t) + \left[\frac{U_t}{q_1} \right]^2 \text{Var}(W_t) + \left[\frac{U_t W_t}{q_1^2} \right]^2 \text{Var}(q_1), \quad (17)$$

where all variables are defined in Equation (11). Variance of W_t was estimated from the biological samples from each research cruise. Variance of U_t was estimated as the variance of U among the four depth strata.

Variance of q_1 was estimated as

$$\text{Var}(q_1) = \left[\frac{U_{85} W_{85}}{B_{80,85}^*} \right]^2 \text{Var}(P_{80}) + \left[\frac{U_{85} P_{80}}{B_{80,85}^*} \right]^2 \text{Var}(W_{85}) + \left[\frac{P_{80} W_{85}}{B_{80,85}^*} \right]^2 \text{Var}(U_{85}) + \left[\frac{U_{85} P_{80} W_{85}}{B_{80,85}^*} \right]^2 \text{Var}(B_{80,85}^*), \quad (18)$$

where all variables are defined in Equation (12). Variances of W_{85} and U_{85} were estimated as described above for W_t and U_t . Variance of P_{80} was estimated as described for $P_{r,t+1}$. Variance of $B_{80,85}^*$ was estimated with the previously described Monte Carlo model.

Abstract.—The inverse method for mortality and growth estimation (IMMAGE) is a new approach to obtain unbiased estimates of mortality and growth parameters for larval fishes from length-frequency data biased by the size selectivity of plankton nets. The performance of IMMAGE is compared with methods which attempt to eliminate selection bias from sampled length-frequencies. Using Monte Carlo simulations, IMMAGE estimates growth and mortality parameters that are more accurate and precise than those produced by other methods.

Inverse method for mortality and growth estimation: A new method for larval fishes

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Estimation of the growth and mortality rates of larval fishes is complicated by the sampling biases that can result from the size selectivity of plankton nets. Size selectivity due to net avoidance by larvae, for example, results in an underestimation of larval abundance that progressively increases with increasing larval length. This bias leads to an underestimation of mean length-at-age and therefore growth rate, because larger larvae in each age-class are underrepresented relative to smaller larvae. Such bias also leads to an overestimation of mortality rate, because older larvae are underrepresented relative to younger larvae. Size selectivity due to extrusion of larvae results in an underestimation of larval abundance that progressively decreases with increasing larval length and likewise leads to bias in estimates of growth and mortality rates.

Growth studies rarely address such size selection, and when they do, the approach taken is usually to devise a sampling procedure that provides unbiased length-frequencies (Methot and Kramer 1979, Yoklavich and Bailey 1990). Mortality studies, by comparison, almost always address

size selection and do so after the fact by taking one of several approaches to eliminate the selection bias from the sampled length-frequencies. One approach taken by mortality studies is to divide the sampled length-frequencies by length-specific estimates of capture probability. Such capture probabilities have been obtained from field studies and estimated as (1) catch ratios of large to small mesh nets (Lenarz 1972, Leak and Houde 1987), (2) catch ratios of day to night sampling (Houde 1977, Zweifel and Smith 1981, Morse 1989, Somerton and Kobayashi 1989), or (3) catch ratios of plankton nets to purse seines (Murphy and Clutter 1972, Leak and Houde 1987). Capture probabilities have also been based on theoretical escapement models (Ware and Lambert 1985). A second approach taken by mortality studies is to simply eliminate the biased portions of the length distribution. Such elimination may exclude only small (Morse 1989) or large larvae (Houde 1977, Methot and Kramer 1979) or both (Essig and Cole 1986). Elimination of biased length-frequencies also has been combined with the use of capture probabilities (Houde 1977, Morse 1989).

Although the various approaches may differ in the specifics of their application, all are based on the premise that length-frequency data must first be corrected for selection bias before they can be utilized to estimate growth and mortality. Here we introduce a new approach which reorders and joins the processes of data correction and parameter estimation. This approach, which is based on a stock assessment technique known as synthesis modeling (Methot 1989, 1990), will herein be referred to as the inverse method for mortality and growth estimation (IMMAGE). The use of IMMAGE is examined to estimate growth and mortality rates from biased length-frequency data. Additionally, the performance of IMMAGE, using Monte Carlo simulation, is compared with approaches used to correct selection bias in length-frequency data prior to parameter estimation.

Materials and methods

IMMAGE vs. bias correction

To understand how IMMAGE works and why it is an inverse method for obtaining estimates of growth and mortality parameters, the bias-correction approach should first be examined (Fig. 1a-d). One variant of the bias-correction approach might include (1) estimating the unbiased length-frequency distribution (Fig. 1b) by dividing the observed length-frequency distribution (Fig. 1a) by length-specific estimates of capture probability; (2) converting the unbiased length-frequency distribution to an age-frequency distribution (Fig. 1c) using age and length information; and (3) estimating the instantaneous mortality rate (M) as the slope of a straight line fit to the logarithms of numbers at age (Fig. 1d).

The IMMAGE approach, if applied to the same data, would include (1) choosing initial values for M and the number of day-0 larvae (N_0); (2) estimating an unbiased age-frequency distribution (Fig. 1e) based on the values of M and N_0 ; (3) estimating the unbiased length-frequency distribution (Fig. 1f) from the age-frequency distribution using age and length information; (4) estimating the observed (i.e., biased) length-frequency distribution (Fig. 1g) by multiplying the unbiased length-frequency distribution by estimates of capture probability; and (5) iteratively varying M and N_0 , and repeating steps 2-4, until the best fit is achieved between the estimated and observed length-frequency distributions.

Thus both approaches estimate M by fitting a mortality model. However, in the bias correction approach, the model is fit to numbers-at-age derived from the observed length-frequencies; while in the IMMAGE approach, the model is fit to the observed length-

frequencies themselves. Growth parameters are estimated by IMMAGE in a similar manner, except a growth model rather than a mortality model is fit to the length-frequencies.

To estimate the observed length distribution, IMMAGE requires specification of a process model and ancillary data. The process model contains parameters that are iteratively varied to achieve the best fit to the observed length-frequency distribution; the ancillary data are parameters assumed to be known. For growth estimation, the process model consists of a growth function describing the mean length-at-age and a variance function describing the variance in length-at-age. Ancillary data include estimates of the capture probability at each length. For mortality estimation, the process model consists of a mortality function describing the instantaneous mortality rate at age or length. Ancillary data include the mean and variance in length-at-age, and the capture probability at each length. Growth and mortality process models are not restricted to any particular form and may include linear or nonlinear functions.

The performance of IMMAGE and several of the bias correction approaches to parameter estimation was examined by using a Monte Carlo simulation model. For growth parameter estimation, bias correction approaches were not examined because no application to larval fishes could be found in the literature. For mortality parameter estimation, three bias correction approaches were examined: (1) elimination of the biased portions of the observed length-frequency distribution, (2) division of the observed length-frequency distribution by estimates of capture probability (correction), and (3) elimination of the biased ages from a corrected age distribution.

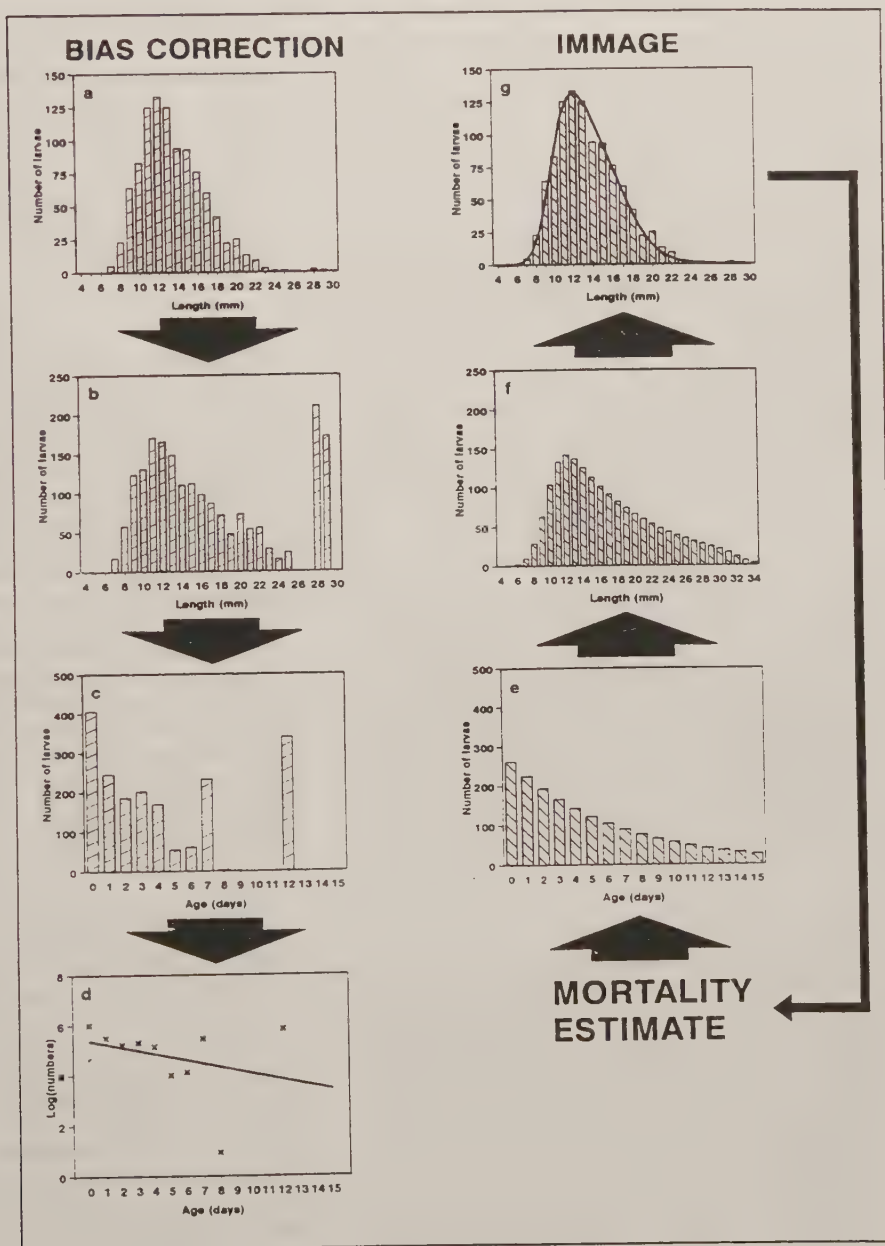
Monte Carlo model

The Monte Carlo simulation model is designed to mimic the sequence of steps typically used in growth and mortality studies. A central feature of this model is the simulated collection of three types of data: length-frequency samples, selection samples, and ageing samples.

Length-frequency samples are either unbiased, representing random samples drawn from a larval fish population, or biased, representing samples collected with a plankton net. Selection samples are two independent length-frequency samples, one biased and the other unbiased, used to estimate length-specific capture probabilities. Such samples represent those that might be produced by an experiment to estimate the length-selection characteristics of a plankton net (i.e., day to night catch comparisons). Ageing samples are length-frequency samples in which each length mea-

Figure 1

Comparison of the bias-correction and IMMAGE approaches to estimating instantaneous mortality rate (M) from selection-biased length-frequency data. Bias correction (left column) begins by dividing (a) the observed length-frequency distribution by estimates of capture probability to estimate (b) the unbiased length distribution. The unbiased length distribution is then converted to (c) an age distribution, and M is estimated with (d) linear regression. IMMAGE (right column) begins by creating (e) an unbiased age distribution using initial estimates of M and the number of day-0 larvae, N_0 . The unbiased age distribution is converted to (f) an unbiased length distribution using the ageing sample. (g) The unbiased length distribution is multiplied by the capture probabilities to estimate the sampled length distribution (solid line), then mortality estimates are varied iteratively to minimize the residual sum of squares between the observed (histogram) and the estimated length distributions.



surement is associated with an age. Ageing samples are considered biased when used in growth parameter estimation but are considered unbiased when used in mortality parameter estimation. This distinction is made because mortality parameters can be influenced by

selection bias in ageing samples as well as by selection bias in the length-frequency samples. To simplify interpretation of the results and avoid compounding the effects of the two sources of bias, bias in the ageing samples has been ignored in the mortality estimation.

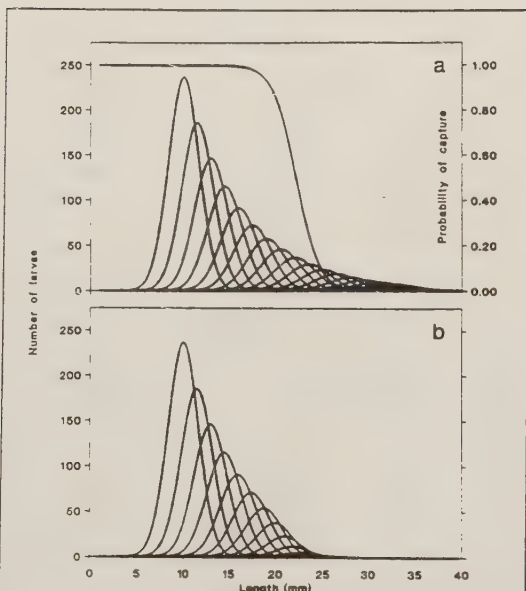


Figure 2

(a) Unbiased length distribution and relative abundance of each age-class in the simulated population of larvae, and the assumed values of capture probability (solid line) and the length of 95% selection (dotted line). With the length elimination method of bias corrector, all lengths to the right of the 95% selector line are eliminated. (b) Length distribution and relative abundance of each age-class within a sample collected with a size-selective plankton net. This distribution is created by multiplying the length distribution shown in (a) by the capture probabilities.

Unbiased length-frequency samples for these three types of data were generated by simulating the random sampling of a larval fish population (Fig. 2a) with a constant daily recruitment, a constant instantaneous daily mortality rate (M) of 0.20, and a length distribution at each age conforming to a normal probability distribution. Mean (l_t) and variance ($\text{Var}(l_t)$) of length-at-age were chosen, for simplicity, to be linear functions of age:

$$l_t = 10.00 + 1.50t, \text{ and} \quad (1)$$

$$\text{Var}(l_t) = 2.50 + 0.25t. \quad (2)$$

where t is age (in days) and l_t is length (in millimeters). Samples were drawn from the cumulative length probability distribution of this population that was constructed by dividing each of the population length-frequencies by the total sample size, then

cumulatively summing across all lengths. Individual lengths within a sample were chosen by determining which category in the cumulative length probability distribution just exceeded the value of a generated uniform random number.

Biased length-frequency samples were generated by simulating the sampling of the model population by using a plankton net, which allowed zero extrusion and produced capture probabilities ($P_{c,l}$) described by an inverse logistic function:

$$P_{c,l} = 1 - \frac{1}{1 + 9.00 \times 10^7 e^{-2.61 l}}, \quad (3)$$

where l is length (in mm) [Fig. 2a; parameters in Eq. (1-3) were chosen arbitrarily and were not intended to represent any particular species or sampling gear]. Samples were drawn by using the same procedure as used for unbiased samples except the population length distribution was multiplied by the capture probabilities (Fig. 2b).

Ageing samples were generated similar to length-frequency samples, but after each length was drawn, an associated age was also drawn by using the cumulative age probability distribution at each length and an additional uniform random number. The sample sizes used in the simulations [1000 length-frequency samples, 300 ageing samples, 600 selection samples, with the biased sample size set equal to the unbiased sample size $\times$ the average probability of capture determined from Equation (3)] were arbitrarily chosen but were similar to those used in Somerton and Kobayashi (1989, unpubl. data).

Growth simulations

Growth simulations examining the performance of IMMAGE consisted of 1000 repetitions of the following sequence. First, a biased ageing sample and a selection sample were generated. Second, capture probabilities were estimated from the selection sample by fitting an inverse logistic function of length, using nonlinear regression, to the ratios of the biased to the unbiased length-frequencies. Third, initial parameter estimates for the growth process model [Eq. (1) and (2)] were obtained from the ageing sample by fitting straight lines to length-at-age and variance of length-at-age. Fourth, the unbiased length distribution of each age-class was estimated as a normal distribution with mean and variance predicted from Eq. (1) and (2) evaluated at the current parameter estimates. Fifth, the biased length-frequency distribution of each age-class was estimated by multiplying the unbiased length-frequency distribution by the estimated capture probabilities. Sixth, parameter estimates for Eq. (1) and (2)

were iteratively varied, and steps 4 and 5 were repeated, until the minimum residual sum of squares (RSS) was achieved. The RSS was defined as

$$\sum_j \sum_i (F_{ij} - \hat{F}_{ij})^2, \quad (4)$$

where F_{ij} and $\hat{F}_{ij}$ are the observed and estimated frequency within the i th length interval and the j th age-class.

Mortality simulations

Mortality simulations examined the performance of IMMAGE and three bias-correction approaches: length elimination, division by capture probabilities, and age elimination. Each of the 1000 repetitions of a simulation began by generating a biased length-frequency sample, an unbiased ageing sample, and a selection sample. For all simulations, except those examining IMMAGE, mortality estimation began with an attempt to derive an unbiased age distribution. If length elimination was used, this was accomplished in two stages. First, an unbiased length-frequency distribution was estimated by eliminating all length categories with a capture probability of <0.95 [based on capture probabilities defined by Equation (3), length-classes 3–18 were retained; Fig. 2a]; a probability of 0.95 was used instead of 1.00 because it is better defined. Second, the age-frequency distribution was estimated from the unbiased length-frequency distribution by using the ageing sample and a procedure known as age-slicing (Mesnil and Shepherd 1990). To do this, lengths from the ageing sample were regressed on the ages, and the fitted linear regression equation was evaluated to determine the length corresponding to each age boundary (i.e., 0.5, 1.5, 2.5 days, and so on). Age-frequencies were then estimated by summing length-frequencies between age boundaries.

If division by capture probabilities was used, the age-frequency distribution was estimated by first dividing the observed length-frequency distribution by estimates of capture probability, then converting the length-frequencies to age-frequencies using age-slicing. If age elimination was used, age-classes with a capture probability of <0.95 at the mean length also were eliminated from the age-frequency distribution (age-classes 0–5 days were retained; Fig. 2a). For all three cases, instantaneous mortality rate was then estimated as the slope of an unweighted linear regression to the natural logarithm of numbers-at-age (Ricker 1975).

For simulations examining IMMAGE, mortality estimation proceeded as follows. First, initial values of M and N_0 were obtained from the ageing sample by fitting a straight line to the logarithm of numbers-at-

age. Second, values of l_t and $\text{Var}(l_t)$ were estimated from the ageing sample by fitting straight lines to length-at-age and $\text{Var}(l_t)$ -at-age, using linear regression, and then evaluating the fitted regression equations at each t . Third, capture probabilities were estimated from the selection sample. Fourth, the unbiased age distribution was estimated as $N_t = N_0 e^{-Mt}$. Fifth, the unbiased length distribution of each age-class was estimated as N_t times a normal probability distribution with a mean equal to l_t and a standard deviation equal to the square root of $\text{Var}(l_t)$. The unbiased length distribution for the population was then estimated by summing the age-specific length distributions over all age-classes. Sixth, the biased (observed) length distribution was estimated by multiplying the unbiased population length distribution by the estimated capture probabilities. Seventh, N_0 and M were iteratively varied, and steps 4–6 repeated, until the minimum RSS was achieved. The RSS was defined as

$$\sum_j (F_j - \hat{F}_j)^2, \quad (5)$$

where F_j and $\hat{F}_j$ are the observed and estimated frequencies within the j th length interval.

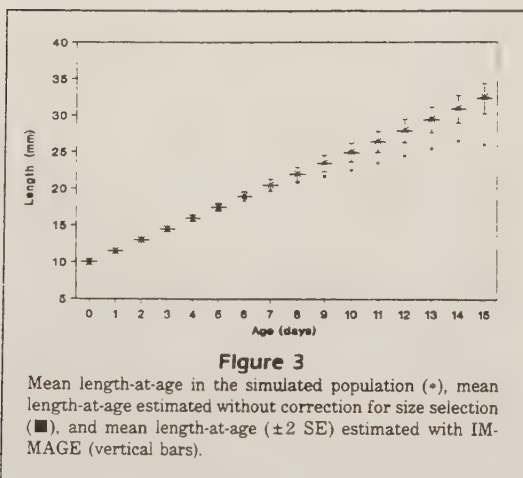
The IMMAGE application used in the simulations (i.e., one that assumes linear growth and constant mortality) is available from the authors as a stand-alone program (IMMAGE, written in Microsoft QuickBasic) designed to run on IBM-compatible microcomputers.

Results and discussion

Growth

The type of size selection examined in the simulations (i.e., a decrease in the probability of capture with increasing larval length) complicates the estimation of growth and mortality in slightly different ways. For growth estimation, the primary effect is that the largest larvae in each age-class are undersampled relative to the smallest larvae, and the mean lengths-at-age are therefore underestimated (Fig. 2b). Since the bias progressively increases with age, plots of mean length against age are curvilinear and falsely indicate a declining growth rate (Fig. 3). Such curvilinear or even asymptotic growth patterns are often reported in studies of wild-caught larvae (Bailey 1982, Laroche et al. 1982, Lough et al. 1982, Thorrold 1988, Warlen 1988). Although there may be biological reasons to expect such a pattern, especially for species with pronounced ontogenetic changes in body form, length-selective sampling may be a contributing factor.

IMMAGE estimates of the slope (1.499 ± 0.005 ; $\bar{x}$ 1000 replicates ± 2 SE) and intercept (10.002 ± 0.012)



of the linear growth function [cf. Eq. (1)] were both unbiased, as were all of the estimates of mean length-at-age over the entire age range (Fig. 3). This indicates that, at least for linear growth, IM-MAGE provides unbiased estimates of growth parameters from biased length and age samples.

Mortality

For mortality estimation, the primary effect of the decrease in capture probability with increasing larval length is that relative abundance is progressively underestimated with increasing age (Fig. 2b). If ignored, such a progressive underestimation would result in positively biased mortality estimates. In the simulated population, for example, mortality estimates obtained from the observed length-frequency samples ($M = 0.450 \pm 0.004$) had a highly significant positive bias of 125% (Fig. 4a).

Elimination of the biased length-frequencies was only partially effective in reducing the bias in estimated mortality rates, because the mortality estimates ($M = 0.364 \pm 0.007$) still had a highly significant positive bias

of 80% (Fig. 4b). In practice, length elimination is likely to be even less effective than it appears here, because it is usually applied to cases where the capture probabilities are crudely known, whereas exact knowledge is assumed in the simulations.

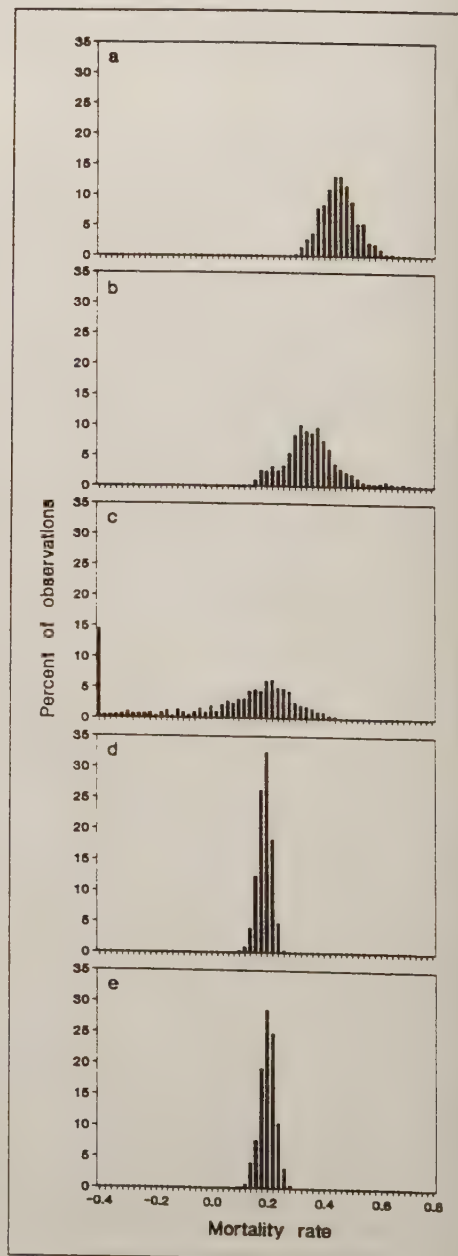


Figure 4 (right)

Frequency distribution of 1000 simulated estimates of instantaneous mortality rate computed from (a) observed length-frequency data, (b) observed length-frequency data after eliminating all length-frequencies with a capture probability of < 0.95 , (c) observed length-frequency data divided by estimates of capture probability, (d) corrected age-frequency data after eliminating all age-frequencies with a capture probability of < 0.95 , and (e) observed length-frequency data using IM-MAGE.

Dividing the observed length-frequency distribution by estimates of capture probability was as ineffective because the mortality estimates (-0.035 ± 0.030) had a highly significant negative bias of 83% (Fig. 4c). The negative bias and the strong negative skew in the frequency distribution are due to the infrequent generation of large larvae. When such larvae occur in a sample, their relative abundance is greatly magnified by their extremely small capture probabilities. The overestimation of large length-classes results in a corresponding overestimation of old age-classes. Because the overestimated age-frequencies are at the extreme of the age range, they exert considerable influence on the slope of the mortality regression and thereby result in the underestimation of M .

Elimination of the biased age-frequencies nearly eliminates this problem and results in mortality estimates (0.192 ± 0.002) with a significant but small negative bias of 4% and a considerable reduction in variance (Fig. 4d). The apparently greater effectiveness of age elimination compared with length elimination is a function of the variance in length-at-age within the larval fish population. For example, when length elimination is applied to the simulated population, essentially all of the undersampled lengths are removed. However, this creates a new bias in the age distribution, because some age-classes experience greater elimination than others (Fig. 2a). Clearly, if no variation exists in length-at-age, length elimination will be identical to age elimination. To our knowledge, the use of age elimination has not been reported in the literature.

Mortality estimates produced by IMAGE (0.201 ± 0.002) are unbiased and, along with age elimination, have the smallest variance (Fig. 4e). This superior performance is achieved because, unlike length or age elimination, IMAGE uses all of the sampled length-frequency data and, unlike correction, uses capture probability multiplicatively and therefore avoids magnifying the sampling error.

Practical application of IMAGE

The application of IMAGE using the Monte Carlo simulation has been chosen because of its simplicity. Although linear growth, constant mortality, and monotonically increasing size selection may not always be suitable for a particular application, the IMAGE procedure is extremely adaptable in the way growth, mortality, and size selection can be specified. For example, growth could be specified as an exponential or a Laird-Gompertz function, and size selection could be specified as a double logistic function (Somerton and Kobayashi 1989) describing extrusion and avoidance simultaneously. Mortality could be specified as either a stage-specific function, where the mortality rates of

yolk-sac and feeding larvae differ, or an inverse function of age (Lo 1986). More importantly perhaps, mortality could also be specified as a function of length.

Although mortality rates of larvae likely decline with length for many species (Pepin 1991), length-dependent mortality rates are difficult to estimate because such mortality induces a progressive bias in mean length-at-age (if the largest larvae in an age-class survive better than the smallest, the apparent growth rate is positively biased; Methot and Kramer 1979). This problem can be circumvented with IMAGE by estimating the size-selected length-frequency distribution using a length-based population model (Somerton and Kobayashi 1990) which mimics the growth and survival of individual members of an age-class over time. Using such an approach, the likelihood of size-dependent mortality could be tested against constant or age-dependent mortality based on goodness-of-fit to the observed length-frequencies.

Several variations on the application of IMAGE described herein may be more appropriate in other cases. First, the estimation of growth and mortality parameters could be accomplished simultaneously rather than separately by allowing the mortality process model to include growth parameters as variables rather than as known quantities. Second, the objective function used for parameter estimation could be specified as a likelihood function rather than a sum-of-squares function. This would be especially appropriate in cases where the errors about the observed length-frequencies are not normally distributed. Third, prior estimates of some parameters could be included in the growth and mortality process models rather than estimating all parameters directly from the three samples (i.e., ageing, length-frequency, and selection samples).

We believe the best way of estimating parameter variances for an IMAGE application is to use a sample reuse technique known as bootstrapping (Efron and Tibshirani 1991), because all sources of sampling variability can be included. Bootstrapping IMAGE, however, is computationally intensive and potentially time-consuming. To facilitate variance estimation on slow computers, we have therefore included in the IMAGE program an approximate technique that is based on the inverse of the information matrix (Ratkowsky 1983).

When obtaining larval fish samples free of selection bias is difficult, IMAGE can still obtain unbiased estimates of growth and mortality parameters. Not only does IMAGE provide estimates that are more accurate and precise than other approaches, its greater flexibility in form allows estimation of length-dependent mortality rates that are perhaps biologically more realistic than the constant rates now estimated.

Acknowledgments

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Effects of the Santa Barbara, Calif., Oil Spill on the Apparent Abundance of Pelagic Fishery Resources

JAMES L. SQUIRE, Jr.

Introduction

Many studies have been made of the effects of oil on marine invertebrates, plants (marine algae and phytoplankton), and vertebrates such as seabirds and marine mammals. An excellent review of these findings, which includes some references to fish and pathological effects of aromatic hydrocarbons, has been published by the Royal Society, London (Clark, 1982). That review dealt with the environmental effects of such major oil spills or releases such as those by the tankers *Torrey Canyon* (119,000 t) on the south coast of England, *Metula* (50-56,000 t) in the Straits of Magellan, *Argo Merchant* (26,000 t) off Cape Cod, and the super tanker *Amoco Cadiz* (223,000 t) on the coast of northern Brittany. Those spills were studied to determine their effect on living resources. In contrast there are few references on the impact of oil spills on pelagic fishery resources.

The release of approximately 240,000 barrels (bbl) (34,800 t) of Alaskan crude oil by the tanker *Exxon Valdez* in Prince William Sound, Alaska, in March 1989, has created increased public interest on the effects of petroleum spills on biological resources.

The largest crude oil spill off California resulted from the blowout of the subsurface oil well casing at the Union Oil Company Platform A in the Santa Barbara Channel (Fig. 1) about 6.5 miles southeast of the City of Santa Barbara, California. This spill started

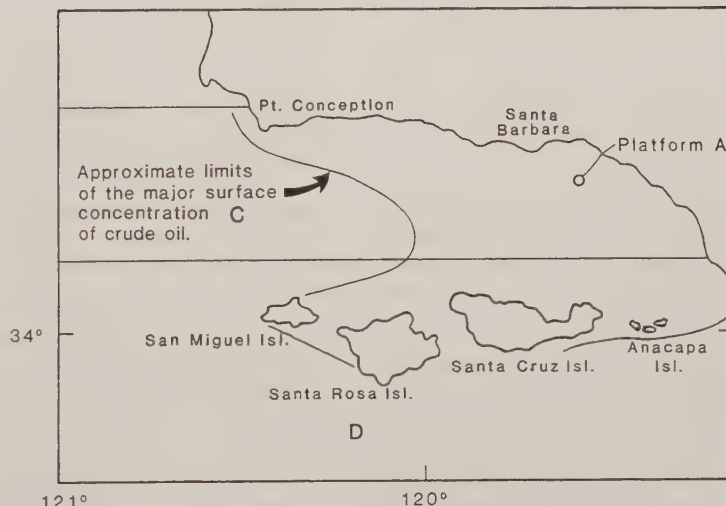


Figure 1.—Approximate limits of major surface concentrations of crude oil.

on 28 January 1969 and continued at rates of up to an estimated 5,000 bbl per day into April 1969 with some discharge of crude oil continuing after this time. A crude oil line break in December 1969 resulted in a spill of additional oil into the Santa Barbara Channel. Extensive areas of crude oil in the Santa Barbara Channel were evident into 1970. The total amount of crude oil spilled at Platform A is unknown and can only be estimated; this is in contrast to the reasonably accurate measurements from tanker spills. A U.S. Department of the Interior publication (Anonymous, 1979) reported estimates of 33,000 bbl (4,782 t) spilled at Platform A; another reference in the same publication estimated 77,000 bbl (11,159 t).

Crude oil on surface waters in the Santa Barbara Channel is not uncommon.

The Santa Barbara Channel and submerged areas about the Islands are known to have several hundred natural subsurface oil seeps. These seeps are variable in their discharge rates and are estimated to have a total spill level of 40-670 bbl per day (Anonymous, 1979). A spill level of 200-400 bbl per day would be a reasonable estimate. At a rate of 300 bbl per day, the natural spill in this area would be over 15,800 t of crude per year. In addition to seeps in this area, other oil seeps are present to the southeast off the southern California coast, some existing in the San Pedro Channel.

The crude oil from the Platform A spill spread throughout the Santa Barbara Channel with major concentrations in the eastern half of the Channel. The surface concentration of crude oil extended offshore to the southeast to

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Anacapa and Santa Cruz Islands in particular (Fig. 1). The distribution of oil on the surface was highly variable after the initial release. Concentrations were continually shifting relative to changes in surface currents.

The area covered by crude oil included one of the more important commercial fishing areas for pelagic fish resources, including the northern anchovy, *Engraulis mordax*; Pacific sardine, *Sardinops sagax*; Pacific mackerel, *Scomber japonicus*; Pacific bonito, *Sarda chiliensis*; and jack mackerel, *Trachurus symmetricus*. Pacific sardine and Pacific mackerel, two important commercial species, were at very low levels of abundance at the time of the oil spill (Squire, 1983).

Surface concentrations of crude oil which spread over the Santa Barbara Channel area affected seine fishing. The oil film and its resulting surface sheen impaired the ability of the boat crews to sight schooling fish. Also, any fish caught would probably have been tainted with hydrocarbons and not desirable for public consumption (McIntyre, 1982). After natural dispersion of the initial oil spill by currents, purse seine operations could be conducted in clear areas. Aerial fish spotters were able to see fish schools swimming below the surface oil slick, and when the fish school would move out from under the oil slick into an area clear of crude oil, purse seining operations could be conducted.

In 1962, several years before the Platform A spill, the National Marine Fisheries Service (then called the Bureau of Commercial Fisheries) started an aerial monitoring program for pelagic fishery resources common to the central and southern California coast (Squire, 1972, 1983). This program utilizes the services of commercial aerial fish spotter pilots who search for the commercial purse seine fleet operating off southern California. The program was operating and collecting data on the relative apparent abundance (Marr, 1951) of pelagic fishery resources in the Santa Barbara Channel and offshore islands area at the time of the Platform A blowout.

This paper reviews the relative apparent abundance of three commer-

cially important pelagic species common to the Santa Barbara Channel and Island areas prior to, during, and for a 3-year period after the oil spill.

Methods

Monitoring Program Procedures

On a flight log sheet, aerial fish spotter pilots under contract to the NMFS Southwest Fisheries Science Center (SWFSC), record information on their flight track, locations of various species observed, and an estimate of tonnage observed. The flight logs are edited and the data are coded into the SWFSC data base. Flight log data were converted to an index of apparent abundance by dividing the tonnage observed by the number of block areas (lat. 10" $\times$ long. 10"—about an 8 $\times$ 10 n.mi. area at the latitude of southern California) entered into during each flight (a measure of observation effort) to give a measure of tons per block area flight (T/BAF). Flight log data represent a sample estimate of the abundance of pelagic species schooling in near surface layers of the ocean surveyed. Flight tracks flown by the spotter pilots are nonrandom, being determined by previous experience regarding the most likely locations for sighting schools of various species relative to the season of the year, real-time information from other aerial spotters or fishing boats, and other recent experiences. In zones where concentrations of fish are historically found, the same block areas tend to be searched every year. For details of the aerial program see Squire (1972, 1983).

Due to the behavior of schooling fish, some species are observed more frequently and in greater amounts during the day, others at night. Sampling differences during day or night could affect the apparent abundance. The ratio of day to night flight operations, 35% night and 65% day, was similar during the oil spill period as for the total program (1963-88). For night observations, near total darkness is required to observe the bioluminescent glow of plankton organisms being agitated by the fish school. Analysis of time of sighting (day or night) indicates the northern anchovy

and jack mackerel are usually observed in greater numbers and more frequently at night, and Pacific bonito in greater frequency and abundance in the day. However, there may be considerable variation in the day/night ratio of sighting during any one year. During the period 1966-72 (before, during, and after the oil spill), 72% of the flight effort was during the day, and 28% was during the night in the Santa Barbara Channel and Islands area (Zones C and D, Fig. 1). In 1969, the year of the oil spill, only a small difference in day/night ratios was noted, with 75% of effort (# BAF searched) during the day and 25% at night. A total of 269 individual survey flights were conducted in 1968, 399 in 1969, and 224 in 1970.

Indices of Abundance

An index of abundance was calculated for each species for groups of block areas or "zones." Zone "C" includes the Santa Barbara Channel and Zone "D" includes the Santa Barbara Channel Islands (Fig. 1). Platform A is located in Zone C, and this zone was the area most affected by the oil spill.

A simple, direct formula is used for the calculation of an index of apparent abundance for each species in the various zones such as Zones C and D, and procedures on calculation are given by Squire (1972, 1983). The index of apparent abundance is expressed in terms of tons per block area flight (T/BAF). Figure 2 gives the amount of search effort (# BAF) for 3 years before and after the oil spill period of 1966-72.

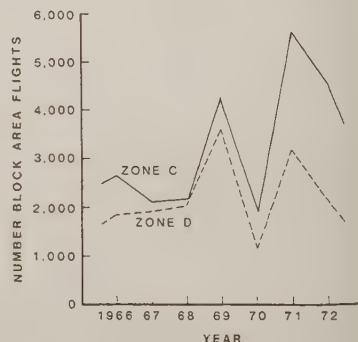


Figure 2.—Number of block area flights conducted in Zones C and D by year, 1966-72.

Results

Distribution of Species Sightings

The geographical distribution of the sightings in the Santa Barbara Channel and about the Channel Islands of the northern anchovy, Pacific bonito, and jack mackerel for the periods 1966-69, and 1970-73 are given in Figures 3-5. Each dot represents the sighting location by a spotter pilot indicating the location of one or more schools (school group) of fish sighted.

Changes in Abundance

Sightings records (1963-88) for the Santa Barbara Channel and Islands areas indicate that the summer-to-winter period has a greater abundance of northern anchovy, jack mackerel, and Pacific bonito. In some years the fishing season for Pacific bonito extends into February or March. The abundance levels of each species of interest are reviewed in the following section by monthly periods before and after the January 1969 oil spill. Flights con-

ducted in the Santa Barbara Channel and Island areas were examined for a 36-month period, 1 year before the oil spill, the year of the oil spill, and 1 year after (January 1968 to December 1970). A total of 269 flights were recorded in 1968, 399 in 1969, and 224 in 1970. Information is given regarding total tonnage observed by month for Pacific bonito, northern anchovy, and jack mackerel (Table 1).

The trend of the abundance index (night index for anchovy and jack mackerel and day index for bonito) for Zones C and D, all sightings, calculated in T/BAF for the three species, 1966-72 is given in Figures 6-8.

Discussion

In contrast to extensive studies on birds and invertebrates, there have been some studies on the effects of the Santa Barbara oil spill on fishes. In February 1969, the NOAA research vessel *David Starr Jordan* sampled the area with plankton nets and found no oil adhering to the fish eggs or any abnormalities in them (Anonymous, 1979).

Samples taken directly under the oil indicated fish larvae were in usual numbers and kinds representative of that area at that time of the year. NOAA concluded that the oil spill at that time had no major discernible effect on the planktonic biota (Anonymous, 1970).

The California Department of Fish and Game sampled pelagic species in the Santa Barbara Channel about 15 days after the initial oil spill and found no evidence of starvation in the northern anchovy that might have resulted from impairment of the planktonic food chain (Anonymous, 1979). No changes from the expected composition of ichthyoplankton were observed. Preliminary information on the results (number of flights and estimates of tons observed) of aerial spotting flights in the Santa Barbara Channel area were made available and were used in development of the conclusion by Straughan (1971) that fish were still present in the Santa Barbara Channel after February 1969. However, no supportive analysis was given relative to changes in abundance before, during,

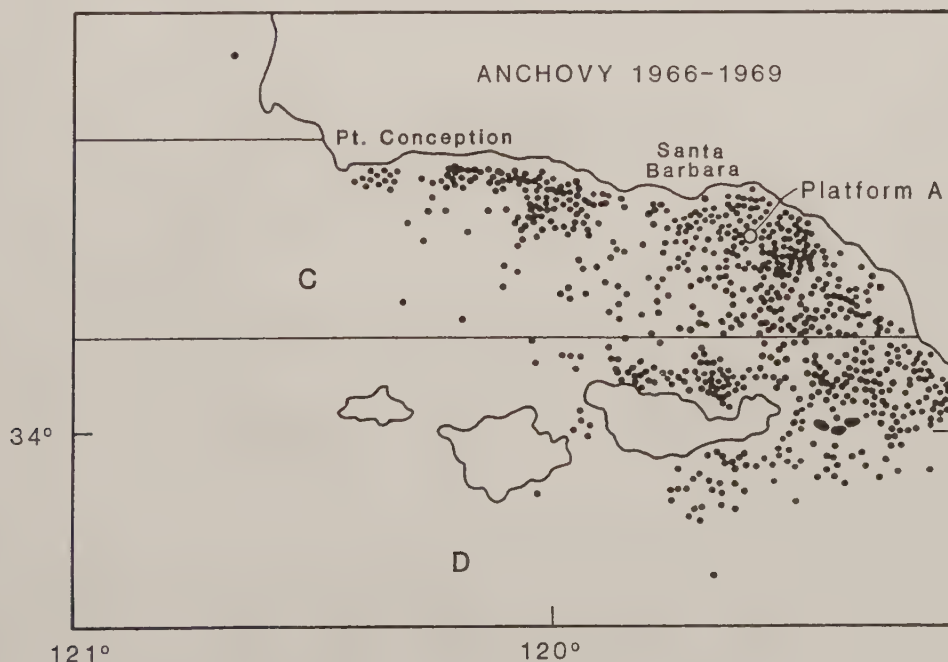


Figure 3a.—Northern anchovy sightings of school or school groups, 1966-69.

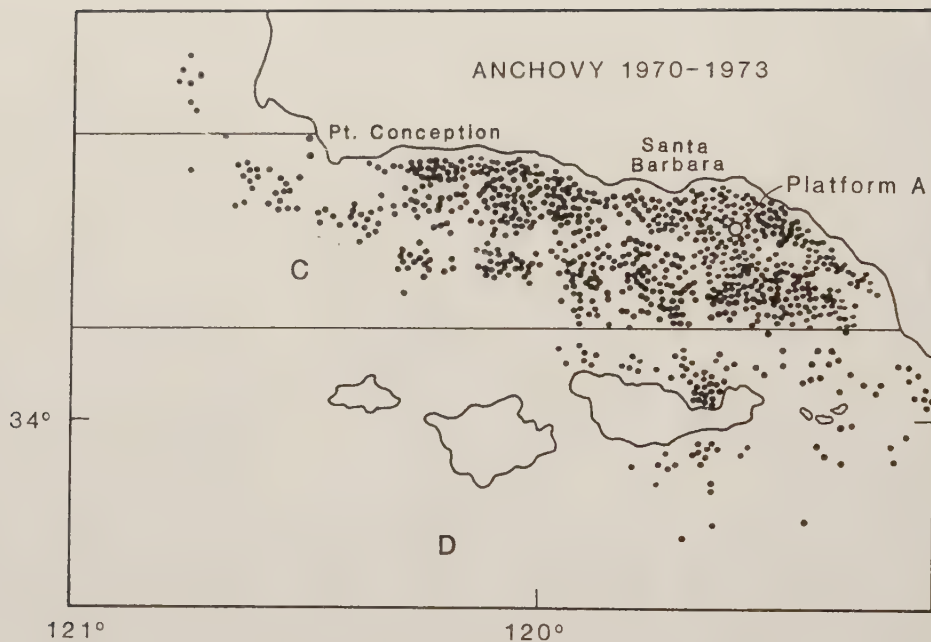


Figure 3b.—Northern anchovy sightings of school or school groups, 1970-73.

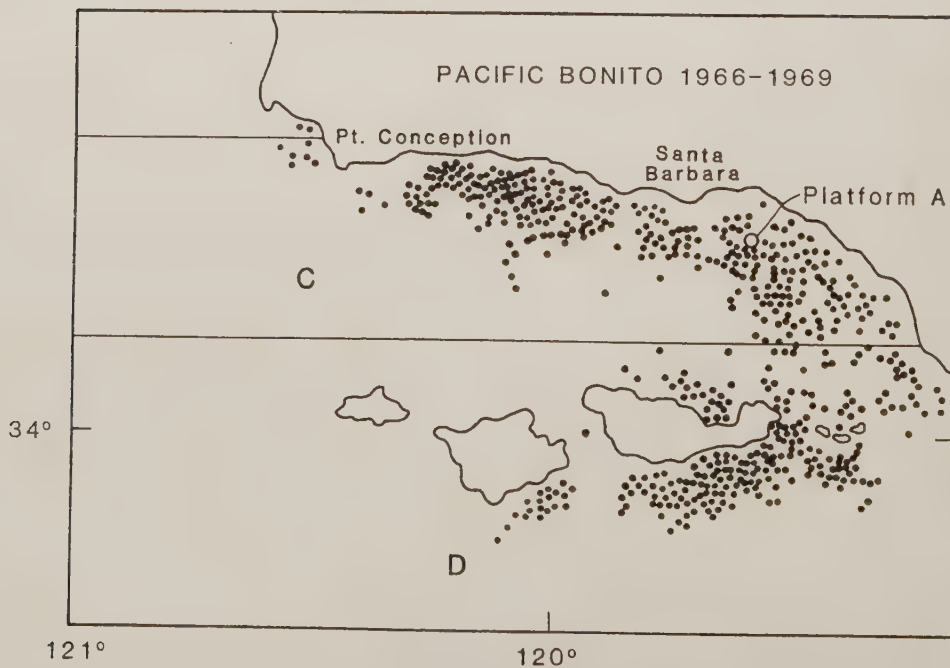


Figure 4a.—Pacific bonito sightings of school or school groups, 1966-69.

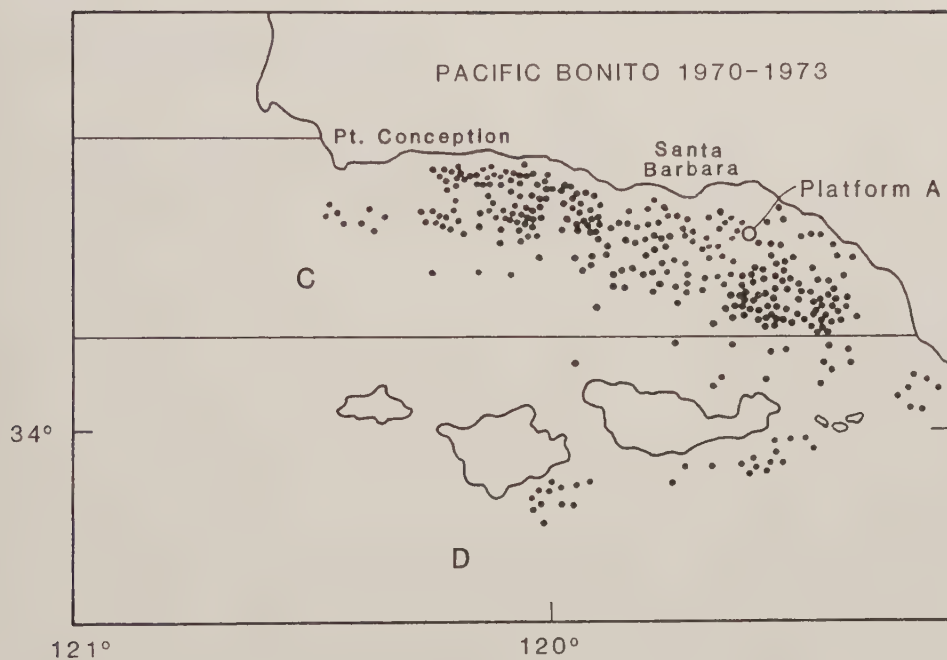


Figure 4b.—Pacific bonito sightings of school or school groups, 1970-73.

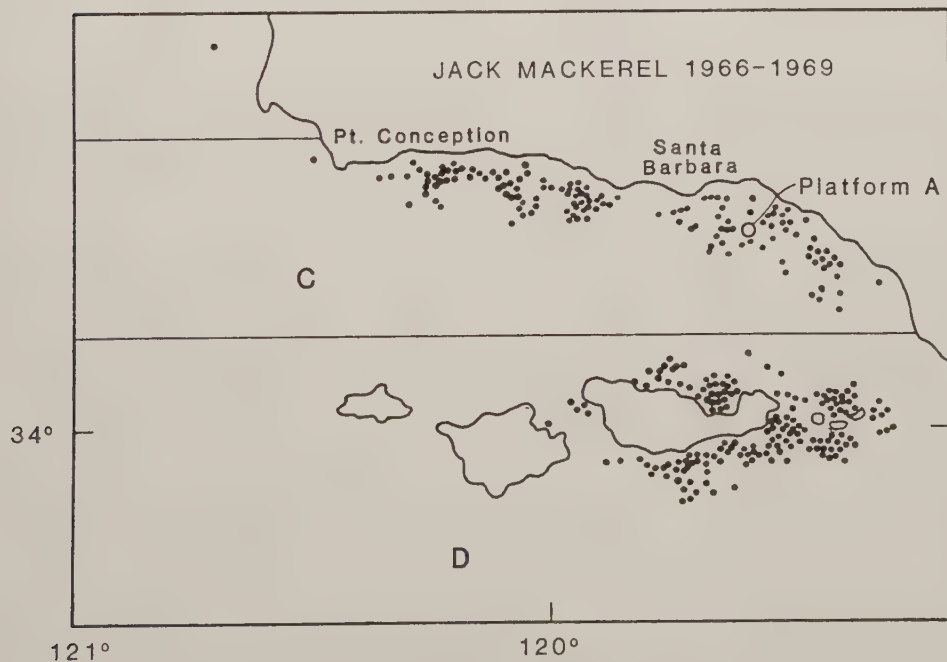


Figure 5a.—Jack mackerel sightings of school or school groups, 1966-69.

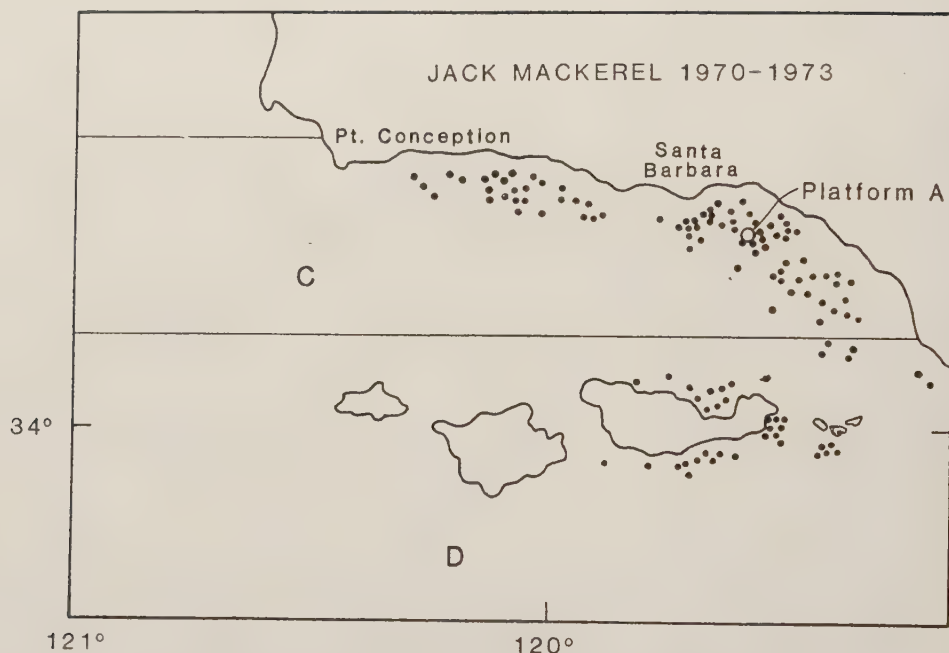


Figure 5b.—Jack mackerel sightings of school or school groups, 1970-73.

or after the oil spill. Straughan (1971) also concluded that the reduction in fish catch was probably due to the problems of fishing in oily waters rather than the lack of fish.

The Platform A blowout spilled a large quantity of crude oil into the waters of the Santa Barbara Channel and Islands. A small amount of crude oil was noted along the coast as far southeast as Newport Beach, Calif. This crude oil spill is the largest recorded in California waters. The major difference between the Platform A blowout and tanker disasters is that the crude oil release from the blowout extended over a period of time in contrast to the short-term release of oil in most tanker accidents.

In addition to the accidental release in 1969, the marine environment of the Santa Barbara Channel and other southern California areas have been subjected historically to a continuing seepage of crude oil into the water column. What effect this has had in the pelagic fishery resources and other biological resources common to the area is un-

known. The pelagic species with which this paper is concerned are commonly found in the Channel, primarily in the eastern half and about the Islands as the sighting graphics (Fig. 3a-5b) would indicate. In an analysis of the aerial monitoring program (1963-89) (Squire¹), "core areas" of distribution and abundance were defined for each species. Zones having considerable crude oil release are included in the core areas for Pacific sardine, northern anchovy, Pacific mackerel, Pacific bonito, and jack mackerel. This analysis would indicate that the natural oil seepage is not having substantial negative effect on the distribution of these pelagic resources.

The results of aerial spotting records for Zones C and D (Fig. 6-8) and monthly summaries of tonnages from

flight observations in the Santa Barbara Channel and Islands area, (Table 1) are reviewed for Pacific bonito, northern anchovy, and jack mackerel.

Northern Anchovy

After the oil spill at the end of January 1969, the northern anchovy was absent in February but was observed during the late spring early-summer months at higher abundance levels than observed in either 1968 or 1970; however, the abundance level showed a decline in 1970 (Table 1).

The trend of abundance index (day index, T/BAF) for Zones C and D are given in Figure 6. Zones C and D are zones where high abundance index levels of anchovy are normally observed, with Zone C an important area for the northern anchovy. Zone C peaked in 1967 with a low in 1968, but increased during the oil spill year, 1969. Zone D peaked in 1968 with a low index level in 1969. Both Zones C and D were at lower levels in 1970, increasing in 1971 (Fig. 6).

¹Squire, L. 1992. Apparent abundance indices for six pelagic species—1962-1990, as determined by an aerial monitoring program. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Admin. Rep. LJ-92-12, 15 p.

Table 1.—Summary of individual aerial fish spotting flights (1968-70) for the Santa Barbara Channel and Islands (for Zones C and D combined) and the estimated tonnage sighted, by month, from records of five spotters.

Year	Distribution of individual flights	Estimated tonnage ¹ sighted		
		Bonito	Anchovy	Jack mackerel
1968				
Jan.	31	4,042	1,450	22
Feb.	29	1,892	4,100	140 C
Mar.	23	203	840	87
April	0			
May	9	0	70	651
June	20	0	2,670	198
July	21	245	4,506	974
Aug.	32	1,650	595	539
Sept.	53	3,784	3,978	1,085
Oct.	17	166	55,000	210
Nov.	18	445	149,800	0
Dec.	16	1,400	46,900	10
	269			
1969				
Jan. ²	13	1,799	7,000	415
Feb.	14	0	0	30
Mar.	28	0	39	1,610
April	19	0	435	602
May	20	0	20,310	142
June	34	5	76,236	580
July	52	399	101,036	2,071
Aug.	58	2,531	649	106
Sept.	28	348	53,130	260
Oct.	48	4,350	26,885	40
Nov.	45	525	80	683
Dec.	40	999	51,560	287
	399			
1970				
Jan.	23	310	4,030	885
Feb.	23	0	207	1,104
Mar.	37	0	3,614	865
April	24	0	4,100	315
May	19	0	8,406	84
June	18	2	11,750	305
July	12	10	8,452	4
Aug.	17	1,221	2,113	17
Sept.	17	2,627	13,130	14
Oct.	13	1,103	4,799	43
Nov.	12	484	945	6
Dec.	9	851	522	0
	224			

¹Short tons.

²Oil spill started January 28, 1969, continued unchecked to April 1969, and continued a minor flow until late in the year.

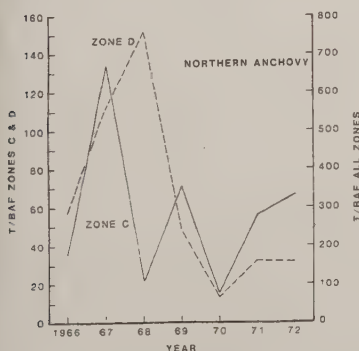


Figure 6.—Trend of abundance in T/BAF for northern anchovy (night index) in Zones C and D, 1966-72.

Jack Mackerel

The jack mackerel resource has a distribution of older adults generally offshore from which the younger year classes recruit into the southern California fishery. The jack mackerel tonnage decreased after the spill, but, overall, increased slightly in 1969, then decreased in 1970 (Table 1). For Zones C and D the index of apparent abundance (night index, T/BAF) was at a low level in 1968 prior to the oil spill and remained at a low level after 1969 through 1972 until showing an increase in 1975 (Fig. 7) (Squire, 1983).

Pacific Bonito

The Pacific bonito fishing season in the Santa Barbara area usually extends from the summer months into the following winter months of February or March. The 1967-68 fishing season ended in February/March 1968. Starting in August 1968, prior to the oil spill, these high abundance levels extended through January 1969, with very high levels just prior to the oil spill. After the oil spill, Pacific bonito were not observed, but they were again observed in increased abundance in July/August 1969, about the same months as initially observed in 1968. Abundance levels remained up until January 1970. Again in 1970, as in previous years, Pacific bonito were absent from February to May with a substantial increase in abundance noted in August (Table 1).

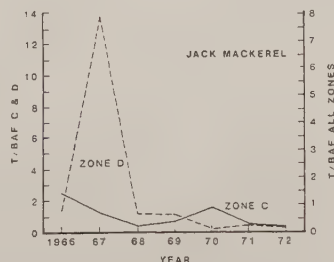


Figure 7.—Trends of abundance in T/BAF for jack mackerel (night index) in Zones C and D, 1966-72.

The apparent abundance index trend (day index, T/BAF) of Pacific bonito in Zones C and D (Fig. 8) follows a steady overall decline (1966-70) in its apparent abundance index prior to the oil spill. The declining trend then shifted to an increase in apparent abundance starting in 1971 and continued into 1972.

Conclusions

A review of the trends of abundance index as calculated for Zones C and D (Figs. 6-8) and of tonnages sighted during observational flights prior to, during, and after the Platform A blowout (Table 1), indicates that the oil spill had some immediate short-term (monthly) negative effects on the apparent abundance of Pacific bonito and jack mackerel. The northern anchovy abundance index in the important Zones C and D were relatively stable from 1968 through 1971, particularly for Zone C, one of the more important zones for evaluating changes during the oil spill period.

The variability in the occurrence and concentrations of pelagic species is difficult to measure and is confounded by variables in the abundance and behavior, the fishes' relation to their environment and its changes, interaction with predators, and wide fluctuations in recruitment. The oil spill occurred

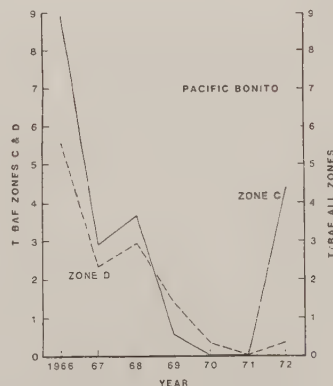


Figure 8.—Trend of abundance in T/BAF for Pacific bonito (day index) in Zones C and D, 1966-72.

in an environmentally unique area where, historically, high levels of crude oil, emanating from underwater oil seepage, are present. Fluctuations in sea surface temperature has a substantial effect on fish distribution. An El Niño event occurred in 1972 and may have been a contributor to increased abundance of Pacific bonito and movement of the northern anchovy in more northern waters including the study area. However, abundance index values during the oil spill year of 1969 do not indicate any unusually reduced fish abundance levels resulting from the oil spill.

Observations during the oil spill period indicated that schools of anchovy, bonito, and jack mackerel were in the normal geographical areas of distribution within the Santa Barbara Channel and Islands, and that their behavior,

below the oil slick was normal relative to depth, movement, and school shape². Data would indicate that pelagic fish resources, with their capability of moving widely in their environment, do not suffer short-term debility from localized oil spills, such as the type that occurred during January 1969 in the Santa Barbara Channel.

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Productivity measurement in common property resource industries: an application to the Pacific coast trawl fishery

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This article measures total factor productivity in industries that exploit resources held in common. Particular attention is paid to the valuation and specification of in situ common-property resources in a neoclassical production technology, catchability of the resource, and variations in economic capacity utilization. An empirical analysis of the open-access Pacific coast trawl fishing industry demonstrates that disentangling the productivity residual from changes in resource abundance, its catchability, and variations in capacity utilization hones the productivity residual to finer precision, lowering mean productivity growth by about half. Removing biological noise from highly variable resources is also important. The results are related to a program limiting the number of vessels and can contribute to sustainable resource management whenever resources are held in common.

1. Introduction

■ In industries using common-property natural resources, productivity measurement faces the thorny problem of accounting for the nonpriced contributions from these resources. When changes in the abundance of the resource stock are not disentangled from measures of productivity or technical progress, results will be biased.¹

The crucial factors for studies of productivity or technical progress in these industries are the proper specification and valuation of the common-property resources in a production technology and the related issue of market failure and external diseconomies to firms. In turn, these factors depend upon the structure of property or access rights, the level of aggregation of the analysis (the firm or society/industry), and the stock-flow relationship between the resource stock and its extractive activity. Smith and Krutilla (1982), Smith

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¹ Empirical studies of productivity growth or technical progress when resources are held in common neglected either the role of resource abundance, the issue of property rights and access, or recent advances in productivity measurement and economic index numbers. Squires (1988, 1991) reviews this literature.

(1980), Brown and Field (1978), and Fisher (1979) touched upon these concerns, but they have yet to be fully developed.

This article develops a framework for measuring total factor productivity (TFP) in industries that exploit renewable resources held in common, paying particular attention to the valuation and specification of resources in a neoclassical production technology. I modify the method of growth accounting and economic index number construction to accommodate the resource and to measure productivity growth in the Pacific coast trawl fishery. Accounting for changes in resource abundance, its catchability, and capacity utilization hones the productivity residual to finer precision, lowering it by about half.

Evaluating productivity growth in a common-property resource industry raises the issue of interpretation. Smith and Krutilla (1982) suggested that technical change or productivity growth in these industries can be a mixed blessing. It might merely hasten rent dissipation and resource decline beyond the economic optimum level—already exacerbated by excessive exploitation under open access. Yet the problem of superfluous inputs, made even more excessive through productivity increases or technical change, differs little from that of inputs made redundant in other industries. The key consideration may instead be a suitable program of public policies, rather than the absence of technical advance or productivity growth.

Sustainable resource use is also of increasing concern. Many of these resources are renewable and held in common, and their exploitation contributes to economic growth in a number of countries. Proper specification and valuation of these resources in production technologies are necessary before the appropriate economic research and policies can be formed or indices of economic growth, performance, productivity, or sustainability developed.² In addition, productivity-enhancing policies, coupled with sustainable resource management, boost profits and maintain cost competitiveness in global markets without resorting to temporary advantages from exploitation rates that are not sustainable at some optimum stock level.

Section 2 discusses specification and valuation of the common-property resource stock. Section 3 discusses the optimization problem for both the sole owner and open access, and it relates these results to corresponding total factor productivity measures. The effects of regulation, catchability of the resource stock, and capacity utilization are also evaluated. Section 4 describes the industry, data, and index number construction. Section 5 reports the empirical results, sources of technical change, and implications for license limitation programs. Section 6 provides concluding remarks.

2. Specification and valuation of the resource stock

■ Common-property natural resources traditionally have been treated like any other input in a neoclassical production technology. Beginning with Scott (1954), the common-property resource stock entered the production process as a factor of production and was treated as an asset, particularly as a stock of capital.³ This approach was applied to both renewable and nonrenewable resources.

In an analysis rooted in the theory of the firm, it is inappropriate to treat a common-property resource stock as a conventional input. Instead, this stock is specified as a technological constraint on the individual firm's stock-flow technology because the stock's abundance affects the production environment within which firms operate but remains beyond

² See El Serafy (1991), for example, for a parallel line of research on national income accounting. Ehui and Spencer (1990) develop an index of productivity and sustainability to compare alternative tropical farming systems accounting for soil depletion based upon the results of the present article.

³ For example, Scott (1954) states that in the short run (within a single season), the fish population is one of the fixed inputs. More recent specifications include Clark (1976), Dasgupta and Heal (1979), and El Serafy (1991).

the control of any individual firm. That is, conventional inputs such as capital, labor, and energy are organized conditional upon expected resource stock abundance levels to generate the extractive flow. Increases (decreases) in resource abundance then shift the production technology, increasing (decreasing) the rate of extractive flow for any given input bundle. McFadden (1978) develops this approach within the framework of the firm's production possibilities set, treating environmental parameters (such as resource abundance) similar to disembodied technical change. Also, the resource stock places a maximum limit upon the extraction rate.

Resource abundance as a technology-shift parameter can be specified in the firm's neoclassical production function. This function, F , expresses the stock-flow relationship between the resource stock and the extractive activity at a given period. F takes the vector of inputs, X , and applies it to the resource stock to extract flow Y , conditional upon the state of technical knowledge t and resource stock abundance level B . It is written $Y = F(X|t, B)$.

An increase in the size of B allows an increase in the flow rate of resource extraction for any given X and t , so that $\delta F / \delta B > 0$. Similarly, technical progress shifts F , given X and t , so that $\delta F / \delta t > 0$. Thus both the abundance of the resource stock and disembodied technological change may be treated as technology-shift parameters.⁴

Gordon (1954) treated fish abundance as a technological constraint in his seminal article on marine fisheries as common-property resource industries.⁵ While this approach does not preclude managing the fishery as if the resource stock were an asset, the framework does properly specify the resource stock just like any other environmental parameter, as a technological constraint, instead of as an input under the control of individual firms.

Proper valuation of the common-property resource stock depends upon the specific property-right structure governing its use. Under competitive open-access conditions, the firm's utilization decision for the resource is not endogenous, and each firm ignores the effects of its production upon the resource stock. Each firm instead behaves as if the resource had a zero user cost, because the effect of a unit change in resource abundance on the open-access firm's profits is zero due to rent dissipation (Gordon, 1954; Smith, 1969; Capalbo, 1986). The firm's marginal costs and the market prices it faces include only the extraction component and not the user-cost component (the latter of which is zero).

In contrast, a sole owner must contend explicitly with the user cost, because the resource utilization decision is now endogenous through the choice of extraction rate and input usage (Capalbo, 1986; Smith, 1969). Social costs associated with the resource externality are now private costs to the firm and, along with extraction costs, factor into the firm's optimization problem (Smith, 1969). Market prices include the marginal user cost of the resource as a component of the full extraction cost. Similarly, the user cost is explicitly considered as a cost when property rights are not assigned but the emphasis is given to social evaluation of productivity growth.

3. The firm's optimization problem and productivity measures

■ Specification of the firm's profit maximization problem depends upon the nature of property or access rights (or aggregation level). I consider both sole-owner and open-access in situ common-property resources. Following standard practice (cf. Clark, 1976), I assume a Schaefer (1957)-type production technology, where each vessel's catch per unit of time is proportional to the resource stock and its costs are inversely proportional to the resource

⁴ Shifts in common-property resource abundance have the same effects upon isoquants for a neoclassical technology as exogenous technological change, since both are changes in technological constraints.

⁵ Thus Gordon (1954, p. 136) states, "For each given level of population, a larger fishing effort will result in larger landings. Each population contour is, then, a production function for a given population level." As Gordon noted, this approach does not preclude the impact of catch increases on reducing the resource stock.

stock. I distinguish noncapital costs and inputs from capital to facilitate capital's role in a later discussion of capacity utilization (CU), but full static equilibrium in all inputs is initially allowed not to confound the discussion of property rights with that of CU. I give only the germane results here, with full development in Squires (1991).

The Lagrangian for the optimization problem of a sole owner (or society) is

$$\max_{Y_t, K_t, B_t} L = \{P_t Y_t - G(Y_t, K_t, W_{jt}, B_t, t) - W_{Kt} K_t\} + \phi_1 [B_t - Y_t] + \phi_2 [B_{t+1} - B_t - h(B_t, Y_t, E_t, U_t)], \quad (1)$$

where P_t is the product price, W_{jt} is the price of the j th variable input X_{jt} , W_{Kt} is the rental or services price of capital K_t , t indexes the state of technical progress (assumed Hicks neutral and disembodied), B_t is the resource stock, $h(\cdot)$ is the biological growth function, Y_t is the current resource extraction rate, $G(Y_t, K_t, W_t, B_t, t)$ is the variable cost function for the optimal combination of variable inputs, where $\delta G / \delta B < 0$, and ϕ_i is the Lagrangian multiplier for constraint i .

The first constraint indicates that the extractive flow from the resource cannot exceed the resource stock itself.⁶ The second represents discrete-time growth of the resource stock. Abundance in time t is determined by its level in the previous period (B_{t-1}), its growth function (h), the resource extraction rate (Y_t), environmental parameters (E_t), and any public regulations (U_t). Not only are Y_t and K_t decision variables to the sole owner, B_t is one as well via the choice of current extraction rate Y_t and the long-run planning decision for K_t (Capalbo, 1986; Smith, 1969). All *ex ante* expectations are assumed realized *ex post*.

The first-order conditions for an interior solution are

$$L_Y = P_t - G_Y - \phi_1 - \phi_2 h_Y = 0, \quad \text{or} \quad P_t - \phi_1 - \phi_2 h_Y = G_Y \quad (2a)$$

$$L_K = -W_K - G_K = 0, \quad \text{or} \quad W_K = -G_K \quad (2b)$$

$$L_{\phi_1} = B_t - Y_t = 0, \quad \text{or} \quad B_t = Y_t \quad (2c)$$

$$L_{\phi_2} = B_{t+1} - B_t - h(B_t, Y_t, E_t, U_t) = 0, \quad \text{or} \quad B_{t+1} - B_t = h(B_t, Y_t, E_t, U_t) \quad (2d)$$

$$L_B = -G_B + \phi_1 - \phi_2 [1 + h_B] = 0, \quad \text{or} \quad -G_B = -\phi_1 + \phi_2 [1 + h_B]. \quad (2e)$$

Condition (2a) states that the harvest rate should be selected such that marginal extraction cost $G_Y (= \delta G / \delta Y)$ equals product price less the marginal value of nonextinction ϕ_1 less the marginal rent from additional fish recruits ϕ_2 times the marginal impact of the current harvest rate on the resource stock $h_Y (= \delta h / \delta Y)$. Extinction is generally irrelevant, and ϕ_1 may be set equal to zero.⁷ Sole ownership implies $\phi_2 > 0$, so from (2a), $P_t = G_Y + \phi_2 h_Y$. Condition (2b) gives the reduction in variable costs, $-G_K = \delta G / \delta K$, from using one more unit of capital to produce a given output, or the shadow price of capital.

Condition (2e) demonstrates two benefits from a unit of resource in place at time t (with $\phi_1 = 0$): (1) harvesting costs are lowered and (2) additional value accrues from future growth of the resource stock (Clark, 1976). These two benefits form the user cost, i.e., the opportunity cost to the user of taking a unit of the resource in the present period. Because the analysis is positive, concerned with measuring productivity growth, I do not consider the stationary-state equilibrium conditions for the stock in a normative analysis.

The continuous time Divisia index of total factor productivity using nonparametric growth accounting is

⁶ A referee noted that the inherent dynamic problem was reduced to its static equivalent. In particular, this first constraint suggests $B_t = Y_t$, although including this constraint really implies an equation of motion between the stock and flow instead of an equality. At any one period this distinction is unimportant.

⁷ Extinction is usually unlikely unless biological growth rates are relatively low. When extinction is a real possibility, shadow prices can be measured by the methods of environmental valuation.

$$-\frac{\delta \ln C}{\delta t} = \frac{[P - \phi_2 h_Y] Y}{C} \frac{\dot{Y}}{Y} - \sum_j \frac{W_j X_j}{C} \frac{\dot{X}_j}{X_j} - \frac{W_K K}{C} \frac{\dot{K}}{K} - \frac{\phi_2 [1 + h_B] B}{C} \frac{\dot{B}}{B}, \quad (3)$$

where $C = \sum_j W_j X_j + W_K K + \phi_2 h_Y Y + \phi_2 [1 + h_B] B = PY$ with linear homogeneity, and the dots over variables represent time derivatives.

Equation (3) shows TFP measured as the residual after allocating the growth rate of output among changes in variable inputs, capital, and resource abundance, the latter specified as Hicks neutral and disembodied. The user cost of the marginal unit of the in situ resource, ϕ_2 , is explicitly considered in this sole-owner problem.

In the individual competitive firm's profit-maximization problem, B_t is not a decision variable, so h_B is not relevant, and each firm ignores ϕ_2 . Only indirectly through $h(B_t, Y_t, E_t, U_t)$ do changes in firms' resource extraction rates affect the resource stock level. The productivity measure is a special case of (3):⁸

$$-\frac{\delta \ln C}{\delta t} = \frac{\dot{Y}}{Y} - \sum_j \frac{W_j X_j}{C} \frac{\dot{X}_j}{X_j} - \frac{W_K K}{C} \frac{\dot{K}}{K} - \frac{\dot{B}}{B}, \quad (4)$$

where $C = \sum_j W_j X_j + W_K K = PY$ under constant returns to scale.

The productivity residual is biased without disentangling variations in B_t . In contrast to the sole-owner problem, because B_t is not a decision variable to firms and $\phi_2 = 0$, proportional changes in abundance are simply pared away from the conventional productivity residual without weighting by cost shares in this positive analysis.

Regulation of a competitive open-access fishery can either develop property or access rights or impose production constraints. This section considers constraints on the extraction process for the competitive open-access fishery, since rights-based regulation is related to the sole-owner problem. Market failure remains because rights are underdeveloped, and the analysis remains firm-level and positive rather than normative.

Under a catch quota Y^* , the constraint $Y_t \leq Y^*$ is added to equations (1) and (2) (Denny, Fuss, and Waverman, 1981). The Lagrangian for a binding constraint, ϕ_Y , is the virtual price of the quota (Rothbarth, 1940), and the unit quota rent is $P_t - \phi_Y$.⁹ The first-order condition in the open-access problem is now $P_t - \phi_Y = G_Y$; vessels adjust catch rates until the unit quota rent equals marginal extraction cost. Alternatively, the cost of market failure can be imposed on firms by a landings tax Γ . (2a) is now $P_t = G_Y + \Gamma$; firms adjust the catch rate until price equals private marginal extraction cost plus tax.

With a binding regulation $K_t \leq K^*$, $\phi_K > 0$, production costs increase, and the net services price of capital becomes $W_K + \phi_K$.¹⁰

⁸ A referee noted that for large firms or small industries, the firm takes the behavior of a few rivals as given. This will yield a different rule than equation (4). Experience has shown that under small numbers, fishers often manage the fishery cooperatively, making the sole owner, equation (3), appropriate. Nonetheless, with the exception of highly specialized fisheries harvesting small localized stocks or distant-water fisheries harvesting on a world scale, the open access coupled with definite limitations on firm size creates competitive, atomistic industries, and (4) holds.

⁹ Ultimately, reduced catch helps rebuild the resource stock, which enters the model through $G(\cdot)$ and the growth equation.

¹⁰ ϕ_Y and ϕ_K could be estimated from a mathematical programming model as shadow prices when the constraints include limits on catch and capital, or as virtual prices from duality-based econometric models (see Squires, 1990). Also, production controls might seemingly preclude rent dissipation, implying $\phi_2 > 0$. However, production controls raise production costs (by inducing inefficiency), reduce rent, and do not alter the fundamental cause of rent dissipation, open access. Moreover, because the resource stock is still not a decision variable to individual open-access firms, even with production controls, firms continue to ignore user costs, and equation (4) remains appropriate for a positive, firm-level analysis (modified for $W_K + \phi_K$ and/or $P_t - \phi_Y$). Firms can respond to capital restrictions that limit the number of vessels by expanding the amount of capital on existing vessels. To the firm this is generally productive investment because it increases output, but to society it is usually unproductive (which can be incorporated following Conrad and Morrison, 1989).

Changes in the size of B_t do not affect productivity measures as directly as indicated in equations (3) and (4). An input bundle often catches an increasing proportion of the residual resource stock as B_t declines, due to the concentrating or schooling behavior of many fish species and the nature of the fishing technology (MacCall, 1990). As B_t decreases in size, so does its spatial distribution, but the density of fish over an area or school size changes little. Fishing firms can quickly locate the remainder, even of a heavily depleted stock, and harvest at rates similar to those of a higher stock level.¹¹ Thus the "catchability" of stock is not directly related to B_t 's size and must be adjusted. Following standard procedures (MacCall, 1976), the catchability coefficient weighting B_t 's abundance is a power function (see below).¹²

Productivity measures are biased when output growth comes from changes in capacity utilization of quasi-fixed factors (CU) along with changes in variable factors and productivity (Berndt and Fuss, 1986) and common-property resource abundance. Altering the value and not the quantity of the quasi-fixed factors adjusts the productivity residual for variation in CU with growth accounting (Berndt and Fuss, 1986). Under constant returns to scale for the unregulated competitive open-access fishery,

$$P_t Y_t = G(Y_t, K_t, W_t, B_t, t) + Z_{Kt} K_t = \sum_j W_{jt} X_{jt} + Z_{Kt} K_t.$$

Rearranging: $Z_{Kt} = [P_t Y_t - G(\cdot)]/K_t = [P_t Y_t - \sum_j W_{jt} X_{jt}]/K_t$. The quasi-rent Z_{Kt} is the residual income not accruing to variable inputs per unit of capital stock (Hulten, 1986).¹³

4. The industry, data, and index construction

■ The Pacific coast trawl fishery comprises vessels in Washington, Oregon, and California harvesting a wide variety of groundfish and pelagic fish species and pink shrimp.¹⁴ The three important trawl gear are groundfish (bottom or roller), shrimp, and midwater, the last used by vessels making at-sea deliveries of pelagic Pacific whiting in a joint venture with foreign fleets; production between gears is nonjoint. Vessels flow between the groundfish and shrimp trawl sectors with the rise and fall of shrimp abundance. Larger vessels may also fish in Alaskan waters.

Most vessels are unspecialized and diversified in the species caught. Vessels tend to be small, from 30 to 110 feet in length, to have crews of three for most vessels and seven for the joint venture vessels, and to land in one or more ports, and they may operate full or part time. Most fishing trips last from one to ten days. Few firms are horizontally integrated to multiple vessels. Vertical integration between shoreside processors and vessels also remains limited.

Revenue shares and catch indices by species are reported in Tables 1 and 2. Pink shrimp, Dover sole, rockfish, and Pacific whiting contribute the most revenue. Most species

¹¹ When populations are cropped by harvesting, fish tend to redistribute themselves to best exploit the most favorable habitats. In turn, this tends to maintain the density of their population centered around the areas of favorable habitat, but their total area of distribution contracts from more marginal habitats. Hence, vessels tend to harvest the most favorable locations, maintaining catchability at relatively stable levels, even if populations are declining (MacCall, 1990).

¹² I am grateful to Alec MacCall for raising this issue and suggesting catchability coefficients. In addition, the Schaefer model assumes a uniform distribution of the fish population. As Clark (1976) notes, however, the Schaefer cost function is still suitable when fish concentrations are uneven or when fish school, if it is understood that the units of the resource stock are considered standard school biomass.

¹³ An anonymous referee noted that Z_K could also include the effects of changing economies of scale if constant returns to scale do not hold. It could also include other returns, such as the existence of market power, should these pertain. Tobin's q can be used with multiple quasi-fixed inputs (Berndt and Fuss, 1986).

¹⁴ Trawlers drag a net from the stern of a vessel, haul it in, dump and sort the contents of the catch on the deck, and store it in holds below. Groundfish are demersal fish, i.e., they live on or near the bottom and are not fundamentally migratory. Pelagic fish are migratory and live higher in the water column.

TABLE 1 Revenue Shares

Year	Dover Sole	Other Flatfish	Rockfish	Sablefish	Miscellaneous Groundfish	Pink Shrimp	Pacific Whiting
1981	0.114	0.095	0.258	0.026	0.136	0.284	0.088
1982	0.131	0.109	0.262	0.043	0.156	0.174	0.125
1983	0.138	0.109	0.254	0.037	0.179	0.137	0.145
1984	0.146	0.099	0.240	0.044	0.222	0.067	0.182
1985	0.198	0.140	0.311	0.063	0.053	0.164	0.069
1986	0.125	0.088	0.229	0.049	0.021	0.371	0.118
1987	0.097	0.082	0.201	0.041	0.036	0.432	0.110
1988	0.115	0.081	0.227	0.044	0.054	0.317	0.162
1989	0.107	0.094	0.237	0.041	0.048	0.265	0.208

Source: PacFIN Management Data Base.

TABLE 2 Percentage Annual Output Growth Rates

Year	Dover Sole	Petrale Sole	Other Flatfish	Rockfish
1982	2.97	0.93	1.37	0.37
1983	-0.75	-0.79	-1.32	-8.44
1984	-0.83	-1.04	-0.60	-6.32
1985	1.70	0.34	1.34	-0.03
1986	3.79	-0.70	-1.77	-3.06
1987	-0.75	0.87	0.89	-8.78
1988	0.23	-0.18	-1.09	11.41
1989	1.02	0.02	1.66	2.14
Mean	-0.02	-0.07	0.06	-1.59

Year	Pacific Whiting Groundfish Trawl	Miscellaneous Groundfish	Pink Shrimp	Pacific Whiting Joint Venture
1982	0.05	4.96	-7.72	4.66
1983	0.01	0.89	-11.56	0.90
1984	0.43	1.53	-3.23	1.47
1985	0.30	-49.72	11.31	-11.44
1986	-0.11	-0.10	20.28	8.86
1987	0.20	0.68	8.72	2.99
1988	0.05	-0.87	1.51	3.35
1989	0.29	-0.94	2.74	7.52
Mean	0.15	-5.44	2.75	2.29

Year	Sablefish	Pacific Cod and Lingcod	Aggregate Output
1982	2.12	0.01	0.59
1983	-1.39	-0.13	-3.75
1984	0.41	-0.12	1.37
1985	-0.51	1.84	1.44
1986	-0.98	-3.61	7.18
1987	-0.04	0.06	2.34
1988	-0.83	3.54	3.66
1989	0.15	-1.13	2.98
Mean	-0.13	0.06	1.63

TABLE 3 Percentage Annual Growth Rates of Biomasses

Year	Species: No Catchability Correction					Aggregate		
	Flatfish	Rockfish	Sablefish	Whiting	Shrimp	(1)	(2)	(3)
1982	-1.05	-9.90	-0.07	7.15	-10.42	-5.84	-2.92	-4.78
1983	2.29	-13.42	-0.24	-1.20	-15.59	-14.41	-7.21	-8.91
1984	-4.13	-10.97	-0.33	-0.59	-4.31	-9.75	-4.88	-6.87
1985	-1.00	-5.92	-0.49	-0.65	15.98	7.68	3.84	5.65
1986	-0.98	-4.05	-0.63	4.75	27.27	22.52	11.26	15.02
1987	-0.19	-5.58	-0.41	-1.37	11.09	6.17	3.09	4.70
1988	-0.52	-9.84	-0.18	-2.86	1.91	-3.51	-1.75	-1.67
1989	-0.66	-1.60	-0.23	-3.44	3.56	-0.97	-0.48	-0.22
Mean	-0.78	-7.66	-0.32	0.22	3.69	0.24	0.12	0.37

Notes: (1) No catchability correction for aggregate biomass index.

(2) Uniform square root catchability correction.

(3) Differential power catchability correction (see text).

were relatively unexploited at the start of the decade but were subsequently harvested at unsustainable rates, causing declining biomass (Table 3).

□ **Data.** The analysis covers 1981–1989, the only years with comprehensive economic and biological data. Squires (1988) gives details for all data and index construction except the biological, which is reported in Squires (1991). Electronic spreadsheets with all calculations and data or summary tables of the raw data are available from the author upon request. The output indices require pounds landed and revenues by U.S. vessels at ports in Washington, Oregon, and California by species. Revenue and landings data are from the PacFIN Management Data Base (PacFIN) of the National Marine Fisheries Service (NMFS). All values are deflated by the GNP implicit deflator.

By 1989, sablefish production faced a consistently binding quota. Hence 1989 sablefish output was valued by $P - \phi_Y$, its implicit unit rent, where ϕ_Y was its virtual price. Coastwide estimates of ϕ_Y were unavailable, but based on a study of a Northern California trawl fishery (Squires, 1990), ϕ_Y was set at 68% of the product price.

Three major inputs are distinguished: labor, capital, and energy. The labor indices are bilateral Tornqvist chain indices for each region for three labor categories: crew, engineer, and captain. Each regional index is aggregated to a fleet index weighting by regional labor-cost shares. This two-step procedure with a superlative chain index gives approximate consistency in aggregation (Diewert, 1978) and captures more accurately coastwide variation in costs and input usage. Each labor category is valued at its opportunity cost for the region's representative home port. The opportunity cost for crew, taken from *County Business Patterns* (U.S. Bureau of the Census), equals the average wage in the retail, transportation, and manufacturing sectors. Engineers' opportunity wage, taken from state reports and from the *Area Wage Surveys* (Bureau of Labor Statistics), equals that of journeyman auto mechanics. The opportunity cost of captains is 20% more than that of crewmembers. The flow of labor services is the number in each labor category multiplied by the number of annual landings from PacFIN.¹⁵

¹⁵ Virtually all trawl vessels use a crew of three. Hence, one person from each labor category is specified. The representative home port of Washington is Westport; of Oregon, Newport; of Northern California, Crescent City; and of Central California, Moss Landing.

TABLE 4 Input Cost Shares

Year	Pacific Trawl Fleet						Groundfish Trawlers		
	Capital Services Price			Quasi-Rent to Capital			Quasi-Rent to Capital		
	Labor	Fuel	Capital	Labor	Fuel	Capital	Labor	Fuel	Capital
1981	0.418	0.180	0.402	0.363	0.156	0.481	0.544	0.163	0.292
1982	0.421	0.175	0.404	0.364	0.152	0.484	0.506	0.169	0.325
1983	0.453	0.157	0.390	0.454	0.158	0.388	0.610	0.189	0.201
1984	0.500	0.137	0.403	0.468	0.140	0.392	0.547	0.168	0.285
1985	0.459	0.156	0.386	0.510	0.173	0.317	0.588	0.198	0.214
1986	0.523	0.088	0.389	0.395	0.066	0.539	0.581	0.082	0.337
1987	0.478	0.098	0.424	0.306	0.071	0.628	0.477	0.086	0.437
1988	0.479	0.090	0.431	0.402	0.076	0.522	0.563	0.095	0.342
1989	0.484	0.098	0.418	0.349	0.070	0.581	0.485	0.086	0.428

Source: See text.

Note: Pacific trawl fleet includes groundfish, shrimp, and midwater joint venture trawl vessels.

The energy index is calculated by an economic-engineering approach. Annual fuel consumption is derived by dividing the annual fuel expenses of a sample of vessels by port-specific diesel fuel prices. Dividing each vessel's annual fuel consumption by its annual landings and averaging over the region's vessels gives the region's mean implicit fuel consumption per landing.¹⁶ Each region's total annual fuel consumption is the product of its mean fuel-consumption rate and number of annual landings. Fuel-expense data come from federal income tax returns, and fuel prices come from quarterly telephone surveys (monthly in later years) of 32 marine fuel docks coastwide for the cash price of 600 gallons of No. 2 marine diesel fuel.

The capital index is a bilateral Tornqvist chain index for the number of vessels in each region for three length classes: (1) 49 feet or less, (2) 50–74 feet, (3) 75 feet and over. Each regional index is aggregated to a fleet index using regional capital cost shares as weights. Vessel counts are from states. The price of capital services, P_K , reflects (1) acquisition cost, from federal income tax returns for vessels built or purchased after the Magnuson Fishery Conservation and Management Act (MFCMA); (2) the interest rate of Moody's seasoned issues for corporate bonds rated Baa (capturing fishing's high risk); and (3) a 7% depreciation rate used by NMFS. Table 4 reports input cost shares.

□ **Resource stock.** The catchability-weighted measure of B_{it} is $B_{it}^{c_{it}}$, where B_{it} is the biomass of species i in time t and c_{it} is its catchability coefficient. The aggregate biomass index is $B_t = \sum_i R_{it} B_{it}^{c_{it}}$, where R_{it} is the revenue share of species i in time t . Recommended estimates of c_{it} were as follows: flatfish 0.9, rockfish 0.5, sablefish 0.7, Pacific whiting 0.5, and pink shrimp 0.7; the more a species schools, the smaller is c_{it} .

Revenue shares are from PacFin (Table 1). Biomass estimates for the ten species are from Pacific Fishery Management Council (1990) or by personal communication with the author. These estimates were derived mostly from population models, usually the stock synthesis model (Methot, 1990) or, occasionally, cohort analysis (cf. Clark, 1976).¹⁷ Trawl

¹⁶ The fuel consumption rates per vessel in gallons per trip by region are (1) Washington, 910.64, (2) Oregon, 657.17, and (3) California, 557.92. The rates reflect the increasing width of the continental shelf and hence increasing trip length from California to Washington.

¹⁷ The stock synthesis model is a large age-structured simulation model where 33 parameters are estimated by maximizing a composite likelihood function based on fishery and fishery-independent data. Cohort analysis uses age-structured models.

surveys of abundance were used in a few instances. Because of the uncertainty with biomass assessments, some degree of uncertainty is introduced into the biomass index. Species without biomass estimates were assumed to change at the same rate as related species.

Pink shrimp biomass is related to environmental parameters rather than the size of resource stock.¹⁸ Hence, biomass is unstable and difficult to estimate, and estimates instead followed a recommended "rule of thumb": 130% of total harvest. All flatfish (flounders, soles) were assumed to change at the same rate as Dover sole (the only flatfish with complete biomass estimates). The aggregate rockfish index comprised widow rockfish, Pacific ocean perch, bocaccio, chilipepper, yellowtail, canary, and thornyheads. It was constructed in two stages to incorporate qualitative information when quantitative information was unavailable and to allow for wide diversity of behavior and habitat.

□ **Tornqvist productivity index.** A discrete-time approximation to the continuous Divisia index of (4) is given by the Tornqvist approximation. This index for an unregulated open-access fishery allowing for variations in CU and resource abundance becomes

$$\ln(TFP_t/TFP_{t-1}) = 0.5\sum_i(R_{it} + R_{i,t-1}) \ln(Y_{it}/Y_{i,t-1}) - 0.5\sum_j(S_{jt} + S_{j,t-1}) \times \ln(X_{jt}/X_{j,t-1}) - 0.5(S_{Kt} + S_{K,t-1}) \ln(K_t/K_{t-1}) - \ln(B_t/B_{t-1}), \quad (5)$$

where B is the composite index of resource abundance, $R_i = (P_i Y_i)/(\sum_i P_i Y_i)$ is the revenue share for output i , $S_j = (W_j X_j)/(\sum_i P_i Y_i)$ is the cost share for variable input X_j , and $S_K = (Z_K K)/(\sum_i P_i Y_i)$ is the capital cost share allowing for variations in CU.

5. Empirical results

■ The empirical results for the open-access Pacific coast trawl fishery demonstrate the importance of adjusting the multifactor productivity residual for variations in (1) capacity utilization, (2) resource abundance, and (3) the catchability coefficient. Failure to make these adjustments biases productivity measures.

Biomass growth (Table 3) indicates generally declining Pacific whiting biomass, punctured by occasional increases, reflecting young age at maturity and the sporadic recruitment of strong year classes of juvenile fish into the fishable stock. The unstable pink shrimp biomass reflects the unstable growth rate due to fluctuations in environmental parameters. The overall biomass index is strongly influenced by whiting and pink shrimp due to their large, fluctuating biomasses and revenue shares.

The rockfish, flatfish, and sablefish growth rates (Table 3) reflect the steady, prolonged decline in biomass due to unsustainable catch rates (Table 2) greater than the slow net growth of the biomass (this reflects long lives, slow growth, and steady recruitment rates).

The late 1970s and early 1980s were generally years with $CU > 1$ (Table 5). Production expanded moderately (Table 2) because the domestic fleet no longer faced foreign competition following the MFCMA of 1977 (which restricted foreign fishing and created exclusive fishery zones out to 200 miles) and because several resource stocks (particularly rockfish) were harvested at rates exceeding maximum sustainable yield (MSY). New vessels were constructed, increasing fleet size and aggregate input use (Table 6). Around late 1982, pink shrimp virtually disappeared because of El Niño (which substantially altered ocean temperature), and output and input prices declined (Table 7). The quasi-rent to capital was less than the capital services price, i.e., $Z_K < W_K$, and $CU < 1$ (Table 5). Bankruptcies

¹⁸ Shrimp abundance fluctuates unpredictably from year to year. Because shrimp are short-lived (3–4 years), a very strong or weak year class can change greatly the total biomass (year classes differ by as much as tenfold). Spawning depends primarily upon environmental parameters rather than the existing spawning stock, i.e., there is not a clearly defined relationship between female spawning biomass and recruitment.

TABLE 5 Capital Prices and Capacity Utilization per Vessel in the Pacific Coast Trawl Fishery, 1981–1989

Year	Capital Services Price (W_K)	Quasi-Rent to Capital (Z_K)	Capacity Utilization
1981	60,535	79,487	$CU > 1$
1982	62,859	84,067	$CU > 1$
1983	55,405	53,041	$CU < 1$
1984	56,082	51,096	$CU < 1$
1985	53,501	38,002	$CU < 1$
1986	47,628	82,228	$CU > 1$
1987	56,728	116,133	$CU > 1$
1988	57,535	77,486	$CU > 1$
1989	55,437	96,756	$CU > 1$

Note: 1981 dollars. Mean per-vessel values.

increased, and a number of vessels went idle or left the fleet (Table 6), transferring activities to Alaska, or were sunk or burnt; disinvestment occurred with a lag.

Around 1985–1986, overall biomass began to rebuild, primarily from a dramatic resurgence of the high-priced pink shrimp (as El Niño subsided) and a growth in Pacific whiting biomass (Table 3). Real fuel prices and interest rates also dropped, while real output prices for most species rose, except for a dip in 1988 (Table 7). Hence, $Z_K > W_K$ and $CU > 1$, signalling investment incentives (Table 5). Fleet size and aggregate input (Table 6) responded: it expanded, albeit only with a lag, and jumped by 6.3% in 1987.

In 1988–1989, the overall biomass declined slightly due to a plunge in rockfish abundance beginning in 1987 and a decline in Pacific whiting (Table 3), and output prices dropped in 1988 but climbed in 1989 (Table 7). Z_K fell by 36% but remained above W_K , CU remained above one, and the fleet size remained stable.

In sum, CU signalled private investment incentives for most of the decade, but the fishery was overcapitalized from a social perspective due to the open-access externality, and harvesting rates were often greater than MSY . By the decade's end, most resources had fallen to near or below MSY levels with stable or declining trends.

Table 8 reports total factor productivity measures. There are no adjustments for changes in resource abundance in columns 1 or 2. Column 1 measures productivity assuming full equilibrium of capital. The combined effect of technical progress and resource abundance

TABLE 6 Aggregate Input Growth Rates

Year	Washington	Oregon	Northern California	Central California	Fleet Aggregate
1982	-10.30	2.53	20.52	3.27	7.12
1983	4.25	3.38	-11.15	-10.93	0.14
1984	-9.40	-7.48	-2.49	-9.11	-7.24
1985	-2.45	-6.87	5.90	19.81	0.67
1986	4.93	1.91	-14.76	-34.99	-2.75
1987	5.70	9.50	5.21	-28.40	6.33
1988	6.91	-7.55	-3.96	-8.41	-4.00
1989	-2.61	8.85	0.02	-0.40	4.65
Mean	-0.37	0.53	-0.09	-4.96	0.61

Note: Tornqvist bilateral chain index. Percentage growth rate. Full static equilibrium of capital not imposed. Capital valued by quasi-rent rather than capital services price.

TABLE 7 Implicit Aggregate Output and Input Price Indices

Year	Output	Input
1981	1.000	1.000
1982	1.042	1.003
1983	0.839	0.876
1984	0.886	0.940
1985	0.957	0.926
1986	1.201	1.030
1987	1.385	1.020
1988	0.662	1.016
1989	1.199	0.938

Note: Formed by Fisher's factor-reversal test.

changes in column 1 indicates two cycles of declines followed by increases in productivity. Column 2, which adjusts for CU variations, shows reduced productivity growth, dampened fluctuations in growth rates, and a more complex pattern.

Excluding resource growth will bias productivity measures. Column 3 of Table 8 reports TFP incorporating variations in CU and biomass but not catchability. In years of declining biomass, such as 1981–1984 and 1988–1989, TFP is otherwise understated. Similarly, when biomass increases, such as during 1985–1987, the greater ease of finding and catching fish, unless accounted for in this stock-flow production technology, overstates TFP growth. Annual productivity growth can also reverse signs unless resource growth is included.

Adjusting the biomass estimates for variations in catchability in column 4 of Table 8 generally dampens the effects of changes in resource abundance upon productivity growth and its year-to-year fluctuations. This enhanced stability follows from the density-dependent habitat selection of fish, as discussed above. Mean productivity growth is about half after the full set of corrections.

Productivity growth over the decade averaged a disappointing 0.65%. The productivity growth rate over 1981–1984, years of declining biomass in all species, averaged a strong 5.33%. Growth averaged -2.15% over 1985–1989, years of rising overall biomass (or modest declines but nonetheless falling for all species except shrimp).

TABLE 8 Total Factor Productivity Growth in the Pacific Coast Trawl Fishery, 1981–1989

Year	No Correction ^a (1)	Capacity Utilization Correction ^b (2)	Capacity Utilization and Biomass Correction ^c (3)	Full Correction ^d (4)
1982	-8.139	-6.538	-0.700	-1.755
1983	-5.028	-3.889	10.526	5.017
1984	9.623	5.871	15.622	12.737
1985	2.967	7.763	-6.902	-4.873
1986	14.163	9.928	-12.589	-5.089
1987	-8.916	-3.988	-10.161	-8.689
1988	2.255	7.662	11.171	9.332
1989	1.653	-1.664	-0.697	-1.444
Mean	1.072	1.020	0.783	0.654

^a Long-run equilibrium in capital and no biomass correction.

^b Correction for variation in capacity utilization but not biomass.

^c Correction for variation in capacity utilization and biomass but not for variation in catchability coefficient.

^d Correction for variation in capacity utilization and biomass, and variability in catchability coefficient.

Note: Calculated by Tornqvist bilateral chain indices. Percentage annual growth rate.

TABLE 9 Total Factor Productivity Growth for Groundfish Trawl Only

Year	Multifactor Productivity	Aggregate Output	Aggregate Input	Aggregate Biomass	Capacity Utilization
1982	-10.64	2.88	15.90	-2.39	<1
1983	-11.24	-4.51	7.07	-3.36	<1
1984	11.71	-2.57	-8.05	-6.23	<1
1985	3.18	0.64	-0.37	-2.17	>1
1986	28.79	-4.25	-31.08	-1.96	<1
1987	-12.23	-7.95	6.35	-2.07	>1
1988	10.40	10.35	3.26	-3.31	<1
1989	2.37	2.50	1.78	-1.65	>1
Mean:	2.79	-0.36	-0.64	-2.52	

Note: Differential power catchability correction (see text). Pink shrimp and joint venture midwater trawl vessels excluded. Correction for variation in capacity utilization (see text). Tornqvist bilateral chain indices and percentage annual growth rates.

Productivity in this stock-flow technology ostensibly rose when overall output growth was unsustainable but fell under sustainable harvesting rates. More accurately, however, exploitation rates for most species except shrimp were unsustainable in most years. Growth in productivity and overall biomass were instead driven by, and inversely related to, the large rises and falls in shrimp biomass (responding to environmental conditions) and, to a lesser extent, whiting biomass (due to young age at maturity and sporadic recruitment of large year classes). High revenue shares gave emphasis. Yet their biomass growth and variation, particularly for shrimp, depend largely upon biological and environmental processes beyond the control of regulators or industry. Firms suffer low apparent productivity growth because of the substantial biological noise and the corresponding difficulty in organizing efficient harvesting.¹⁹

To assess productivity growth without the swamping effect from the whiting and shrimp biomasses, all indices were recalculated for groundfish vessels only, the heart of the Pacific trawl fleet. Shrimp biomass was excluded entirely, while whiting biomass was included but weighted by a revenue share excluding joint venture trawlers (groundfish trawlers catch some whiting). Table 9 reports the chain indices and growth rates for productivity, aggregate output and input, and biomass. Productivity growth averaged 2.79%, and the annual variation declined considerably as the biological noise (from pink shrimp and joint venture-caught whiting) was removed from the system. Productivity growth also became consistently positive from mid-decade, except in 1987, when CU and aggregate input surged. These changes followed from the transfer of exiting vessels to Alaska and the resurging shrimp biomass, both of which attracted vessels out of groundfishing. The rate of groundfish biomass decline slowed as well (Table 9). Productivity also grew in response to extensive technical progress (discussed below), even in the face of excessive input use under open access.

The productivity growth rate in both the entire fleet and groundfish-only trawlers displayed considerable annual variation. The ability of mobile vessels to rapidly enter and exit an open-access fishery and switch gear, coupled with fluctuations in resource abundance, generated sharp productivity swings.

¹⁹ Pink shrimp are located in discrete, known beds. However, when vessels repeatedly tow through the area, shrimp progressively disperse and become increasingly hard to find. Shrimp may remain in the general area but do not congregate. Hence, there is much searching, even though discrete grounds are known, and dragging over beds imposes costs that build up over time. Shrimp also respond to variations in light, so shrimp concentrations can vary daily. (Jim Wilen, personal communication.) In short, a good catch one day can be followed by a bad catch the next day, which when coupled with the wide annual variations of biomass, creates substantial inefficiencies.

Future productivity growth rates in the entire fleet may slow and smoothen. Alaska now increasingly offers low returns, so vessels will remain in the overcapitalized Pacific coast fishery, further retarding productivity growth. This was exacerbated when the resurging biomass of high-priced shrimp drew many vessels into the overall fleet.²⁰ Lower interest rates also lessened pressures from vessel mortgages, retaining vessels.

Higher productivity growth may be enjoyed under access control. Without reduced inputs from a vigorous limited-access program, future productivity growth could even fall as vessels face comprehensive catch quotas, as search times for locating new grounds increase, and as transit times to marginal grounds lengthen.

The most important sources of technical progress were electronics and the application of scientific rather than craft principles to vessel and equipment design and to harvesting methods.²¹ Fishing is a semisystematic hunting process for an unseen quarry. Formerly, to locate fish, fishermen had to rely primarily on the experience painstakingly built up over a lifetime. Fishing was also more hampered by inclement weather and seas. However, recent advancements make it harder for fish to hide from their captors, and they also allow higher catch rates, longer seasons, and new fishing grounds.

The rapid introduction of electronic navigation aids (e.g., Loran C and track plotters) and fish finders (chromoscopes and sonar to examine the bottom) dramatically raised the ability to find fish, even by species. Search time decreased as captains returned easily to precise locations of past success or found fish in new locations. The ability to assess the type of bottom (rock, mud, gravel, etc.) allowed more precise net placement, choice of the appropriate net type (e.g., for rocky or muddy bottoms), and selection of the type of fish to harvest (different fish prefer different habitats). Moreover, echo sounders distinguish differences in the air bladders of fish, giving greater control over location, size of fish school, and type of fish to harvest. The quality of electronics has improved substantially and unit costs have fallen rapidly, allowing extensive diffusion.

Gear advances also took place. Nets widened, allowing a greater volume of water to be swept and more fish caught per hour towed. Previously, most rockfish were caught with gear designed for harvesting flatfish. Winches of higher speed and greater capacity allowed larger nets to be released and retrieved at faster rates.

There have also been advances in boat and engine design. Vessels got longer and replaced steel or fiberglass with wood. Marine architects tested models of their designs in computer simulations and in flume tanks. Designs cut down hull drag and gave maximum efficiency. A Kort nozzle gave engines greater thrust, allowing greater fuel economy for net towing and transit.

License limitation programs, which limit the number of vessels, are plagued by the continued increase in productivity and consequent pressures on the resource, even though vessel numbers have been capped. Programs to remove vessels dampen harvesting pressures, but continued productivity growth of the remaining vessels creates countervailing pressures. A recent license limitation program for groundfish vessels could be hampered by productivity

²⁰ Most of the increase in vessel numbers and fishing trips occurred off Washington and Oregon, the predominant shrimping area. From 1985 to 1989, exclusive shrimp vessels increased in Washington from 12 to 38 and in Oregon from 25 to 69. Some otter trawl vessels exited in 1988, after dramatic surges in shrimp biomass from 1984 through 1988 and a general output price collapse (Table 7), but vessel numbers nonetheless remained at historically high levels in these two states.

²¹ In a narrow sense, much of the recent technical progress is embodied technical change, so that vintage effects may theoretically be important. However—because the investment value is relatively small and much of this technical change is related to the managerial function, information, and learning by doing—representing technical change as Hicks neutral and disembodied without vintage effects is satisfactory. See Burnett (1991), Dewees and Hawkes (1988), Crowley (1991), and Squires (1991) for additional discussion on recent technological advancements in the fishery.

growth without compensating vessel reductions, or by eligible shrimp vessels reentering the groundfish sector.

6. Concluding remarks

■ Proper treatment of the resource stock in common-property resource industries is important for measures of productivity or technical progress and, more generally, for technology specification and accurate policymaking. The empirical analysis demonstrated that disentangling the productivity residual from changes in the resource's abundance and catchability and variations in capacity utilization honed the productivity residual to finer precision, lowering the mean growth rate by about half. Biological noise from highly variable, often short-lived resources can affect efficiency and productivity measures.

Unsustainable exploitation rates cropped the biomass of most species from lightly harvested levels to near or below maximum sustainable yield levels by 1989. Overcapitalization, tighter catch quotas, and declining catch rates from excessive inputs under open access may dampen future productivity growth, even in the face of extensive technical progress, unless vessel numbers are reduced by a vessel purchase program or a system of individual transferable quotas.

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Evolution and Biogeography of the Clinidae (Teleostei: Blennioidei)

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The systematic and biogeographic relationships of the teleost family Clinidae (commonly known as kelpfishes or klipfishes), an antitropically distributed group of nearshore fishes characterized by widespread ecological variation, were analyzed using allozyme and morphological characters. The Clinidae comprises three tribes; the matritrophic (ovoviviparous) Clinini and Ophiclinini, and the oviparous tribe Myxodini. Emphasis of the present study was in resolving the relationships among the eastern Pacific Myxodini, which include the South American genus *Myxodes* and the North American genera *Heterostichus* and *Gibbonsia*. Allozyme data were analyzed from 40 presumptive gene loci for all four North American myxodin species, one species of the Australian clinid tribe Clinini (*Heteroclinus whiteleggei*), 10 species (representing all tribes) of the hypothesized sister blennioid family, the Labrisomidae, and two species of the blennioid family Chaenopsidae (also believed to be closely related; the latter two families were used as outgroups).

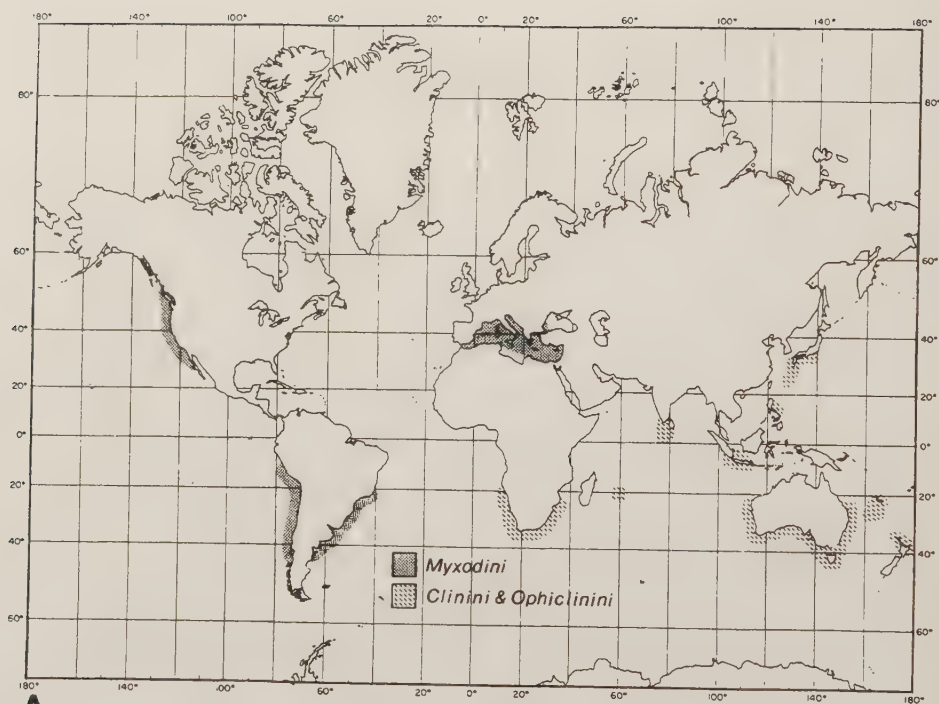
Several different phylogenetic approaches for analyzing allozyme data were used for purposes of comparison, including two frequency character methods, a genetic distance method, a discrete character parsimony method (using only fixed alleles), and a multistate character parsimony analysis (the latter two used presumptive gene loci as characters and selected alleles as character states). Discrete morphological characters were also analyzed both separately and included with allozyme data in parsimony analyses.

Results from morphological and allozyme data, as well as the different methods of phylogenetic analysis, were congruent; yielding identical parsimonious relationships among taxa, except within the genus *Gibbonsia*. Two most parsimonious trees were consistently obtained, which differ in whether *G. metzi* or *G. elegans* is the basal clade within the genus (and the sister group to the other two species). The Clinidae is distinguished by a suite of allozyme character state synapomorphies identified in the present study as well as three morphological synapomorphies. The present study indicates that the cryptotremine labrisomids are the sister group to the Clinidae. The trophodermic matritrophic (ovoviviparous) clinids (comprising the tribes Clinini and Ophiclinini) and the Myxodini are sister taxa, and the South American myxodin genus *Myxodes* is sister to the northern myxodin genera. The North American genera *Heterostichus* and *Gibbonsia* are sister groups.

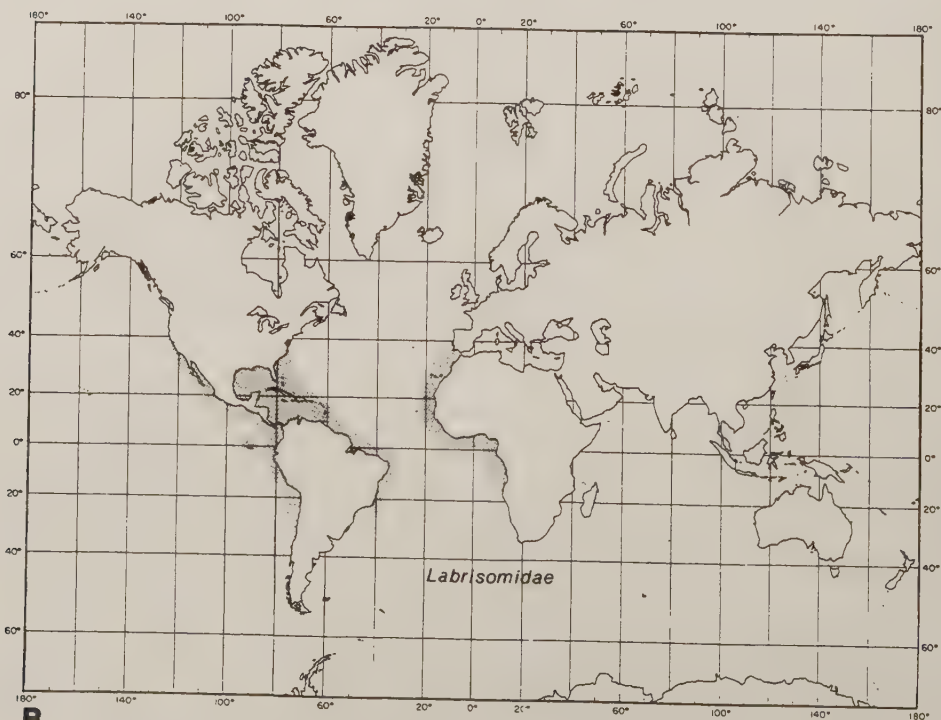
THE systematics of the eastern Pacific members of the teleost family Clinidae, suborder Blennioidei, were last examined by C. Hubbs (1952), and the genus *Gibbonsia* was recently revised by Stepien and Rosenblatt (1991). Clinids are relatively small (less than 300 mm SL, except *Heterostichus rostratus*) benthic fishes, the majority of which inhabit intertidal and shallow subtidal waters (Springer, 1982; Nelson, 1984). George and Springer (1980) redefined the Clinidae, excluding the Tripterygiidae, Labrisomidae, and Chaenopsidae, and adding the tribe Ophiclinini. Clinids are distin-

guished by the morphological synapomorphy of a cordlike ligament extending from the ceratohyal to the dentary symphysis (Springer et al., 1977). The Clinidae contains three tribes (Myxodini, Clinini, and Ophiclinini), 20 genera, and 71 species, most of which are restricted to Australia and Africa (Nelson, 1984). The family has a mostly antitropical distribution, shown in Figure 1A, and all but five (tropical) species are limited to warm temperate waters (Springer, 1982).

The present study primarily examined relationships among the eastern Pacific myxodin



A



B

Fig. 1. Distribution maps of the families Clinidae (A) and Labrisomidae (B), based on C. Hubbs (1952), Penrith (1969), Springer (1970), Stephens and Springer (1973), George and Springer (1980).

TABLE 1. PRESENT STATUS OF THE CLINID TRIBE MYXODINI. (After C. Hubbs, 1952; Springer, 1970; Stephens and Springer, 1973; George and Springer, 1980; and Stepien and Rosenblatt, 1991.)

Component taxa	Common distribution
A. <i>Gibbonsia</i> (Cooper)	
1. <i>G. elegans</i> (Cooper)	Point Conception, California, through central Baja California, Mexico
2. <i>G. metzi</i> C. L. Hubbs	North of Point Conception along U.S. Pacific coast and in areas of cold-water upwelling south through central Baja California, Mexico
3. <i>G. montereyensis</i> C. Hubbs	North of Point Conception and in subtidal waters and areas of cold-water upwelling south through central Baja California, Mexico, including Guadalupe and San Benito islands
B. <i>Heterostichus rostratus</i> Girard	Point Conception through central Baja California, Mexico
C. <i>Myxodes</i> Cuvier	
1. <i>M. viridis</i> Valenciennes	Southern Peru through central Chile
2. <i>M. cristatus</i> Valenciennes	Central through southern Chile
3. <i>M. ornatus</i> Stephens and Springer	Chile, range unknown
D. <i>Riberoclinus eigenmanni</i> (Jordan)	Western Atlantic from southern Brazil through central Argentina
E. <i>Clinitrachus argentatus</i> (Risso)	Mediterranean Sea

clinids. All species in the tribe Myxodini are found in shallow temperate waters of the Western Hemisphere, except for one monotypic genus limited to the Mediterranean Sea (Springer, 1970; Stephens and Springer, 1973). The Myxodini is characterized by ovuliparous oviparity and the lack of an intromittent organ in males; both features are regarded as plesiomorphies (C. Hubbs, 1952; Springer, 1970; George and Springer, 1980). The other clinid tribes, Clinini and Ophiclinini (which are primarily found in South Africa, temperate Australia, and New Zealand), share the synapomorphies of matritrophy (Wourms et al., 1988) and a male intromittent organ (George and Springer, 1980).

Five genera are contained in the Myxodini: *Myxodes*, *Heterostichus*, *Gibbonsia*, *Riberoclinus*, and *Clinitrachus*. Myxodins are not found in Central America or other tropical waters (Springer, 1970; Stephens and Springer, 1973; Nelson, 1984). *Myxodes* ranges along the west coast of South America, from southern Peru through southern Chile. *Heterostichus* and *Gibbonsia* share a distribution from central Baja California, Mexico, to British Columbia, Canada (C. Hubbs, 1952). *Riberoclinus* (monotypic) is found along the southwestern Atlantic coast of South America, and *Clinitrachus* (monotypic)

is a Mediterranean endemic (Springer, 1970; Nelson, 1984; see Table 1 for summary of genera, species, and distributions and Figure 1A for a map of their distributions).

The Labrisomidae has been regarded as either the probable sister group to the Clinidae (C. Hubbs, 1952) or a possible sister group (George and Springer, 1980; Springer, pers. comm.), and 10 species of labrisomids (including all of the six tribes) were used as outgroups in the present study. Evolutionary relationships of the Labrisomidae, based on allozyme and DNA sequence data, are further examined in Stepien et al. (Stepien et al., 1992). Labrisomids are distinguished from clinids by the following morphological characters: scales with radii only on anterior margins, and never small and embedded, but sometimes absent (C. Hubbs, 1952; Stephens and Springer, 1973; George and Springer, 1980). The Labrisomidae contains 102 species and is widely distributed throughout the New World tropics, shown in Figure 1B (Nelson, 1984). A fossil labrisomid is known from Miocene deposits in the Mediterranean, where the family is no longer represented. There are no known fossil clinids (Springer, 1970; George and Springer, 1980).

The blennioid family Chaenopsidae (tube

blennies) was also employed as an outgroup. The Chaenopsidae is restricted to the New World tropics and traditionally has been regarded as most closely related to the neoclinin labrisomids (C. Hubbs, 1952; Stephens, 1963).

Allozyme data from 40 presumptive gene loci of all North American myxodin species and subspecies, as defined by C. Hubbs (1952), were analyzed in the present study. Results from the subspecies and population analyses are presented and discussed in Stepien and Rosenblatt (1991). Allozyme data were also collected from the South American myxodin *M. viridis* Valenciennes and the Australian clinin *H. whiteleggei* Ogilby.

There are several approaches for the phylogenetic analysis of allozyme data, including genetic distance, frequency character, discrete character, and multistate character parsimony methods (Buth, 1984, pers. comm.; D. L. Swofford, pers. comm.). In the present study, four different phylogenetic programs (encompassing all four methods) were used to generate and compare trees.

The relationships of the Myxodini and its sister group, the matritrophic tribes Clinini and Ophiclinini, as well as the relationships of the South and North American myxodin genera and the North American myxodin species, were examined in the present study. Phylogenetic trees based on the allozyme data were compared with those based on morphological characters. Allozyme and morphological data were also combined in parsimony analyses. Several allozyme character state synapomorphies were identified which, in addition to morphological characters, distinguish members of the family Clinidae, the eastern Pacific members of the tribe Myxodini, and the North American myxodin clinids.

MATERIALS AND METHODS

Species and populations analyzed.—Data for the individual clinid subspecies and populations are compared and discussed in Stepien and Rosenblatt (1991), in which *G. erythra* and *G. norae* were placed in the synonymy of *G. montereyensis*. Species, collection locations, and collection numbers of formalin-preserved voucher specimens are given in Materials Examined. The North American Myxodini, as defined by Stepien and Rosenblatt (1991), include *H. rostratus*, *G. metzi*, *G. elegans*, and *G. montereyensis* (Table

1). The diversity of sample sites examined in Stepien and Rosenblatt (1991) represented both the centers of the ranges of each species and areas of infrequent occurrence and sympatry with related species. Allozyme data from the South American myxodin *M. viridis*; the Australian clinin *H. whiteleggei*; 10 species of labrisomids, including *Auchenionchus microcirrhys* (Valenciennes) (tribe Cryptotremi), *Alloclinus holderi* (Lauderbach) (tribe Cryptotremi), *Paraclinus integripinnis* (Smith) (tribe Paraclinini), *P. sini* Hubbs (tribe Paraclinini), *Exerpes asper* (Jenkins and Evermann) (tribe Paraclinini), *Starksia spinipennis* (Al-Uthman) (tribe Starksini), *Labrisomus xanti* Gill (tribe Labrisomini), *Malacotenus gigas* Springer (tribe Labrisomini), *Neoclinus blanchardi* Girard (tribe Neoclinini), and *Mnierpes macrocephalus* (Günther); and two species of chaenopsids, *Emblemaria hypacanthus* (Jenkins and Evermann) and *Acanthemblemaria macropilus* Brock were analyzed.

Enzyme electrophoresis.—Specimens were collected by netting intertidally with use of the anesthetic quinaldine or subtidally by scuba diving and were immediately frozen and stored at -40°C . Separate extracts of eye, liver, and muscle were prepared from each specimen. Tissues were homogenized in a 1:1 volume: volume mixture of tissue and 0.1 M potassium phosphate buffer (pH 7, Waples and Rosenblatt, 1987) and centrifuged at 20,000 g for 10 min. The supernatant fraction was subjected to horizontal starch electrophoresis in 12.5% starch gels (Sigma starch; Sigma Chemical Co., St. Louis, Missouri 63178). Enzymes and tissues surveyed, loci scored, and buffers are given in Stepien and Rosenblatt (1991). Staining methods and recipes were adapted from Selander et al. (1971), Waples (1986), and Buth and Murphy (1990). Enzyme nomenclature follows recommendations of the International Union of Biochemistry (1984).

Relative migration distances were compared with the most common allele (assigned a value of 100) from the population of *G. elegans* at Bird Rock, San Diego, California, from which 63 individuals were surveyed (Stepien and Rosenblatt, 1991). Other alleles were labeled according to the mobility of their products relative to this standard.

Data analysis.—Genetic distance, frequency character, discrete character, and multistate

character parsimony procedures were used to analyze the allozyme data in phylogenetic computer programs to test for method-dependent variation in the generated trees. Different labrisomid tribes and the two species of chaenopsids were designated as the outgroup in separate, independent computer analyses.

Genetic distance clustering procedures are the most widely used approach for analyzing allozyme data but are also the most controversial (Buth, 1984). Genetic distances measure the degree of genetic divergence between each pair of taxa. They lose information by reducing arrays of allozyme frequency data to a single value. BIOSYS-1 vers. 1.7 (Swofford and Selander, 1981, 1989) was used to calculate modified Rogers' (Rogers, 1972; Wright, 1978) genetic distances between all pairwise combinations of taxa. Genetic distances were based on data from one population for each species chosen from the geographic midpoint of their respective ranges. These large population samples included *H. rostratus* and *G. elegans* from La Jolla, California, and *G. metzi* and *G. montereyensis* from San Simeon, California. Data from several other populations for each species, representing other areas of their ranges, were analyzed in Stepien and Rosenblatt (1991). BIOSYS-1 (Swofford and Selander, 1981, 1989) was also used to construct distance Wagner trees (Farris, 1972), which utilized the modified Rogers' genetic distances and the Wagner clustering procedure. Data from 10 species of labrisomids and two species of chaenopsids were included in this analysis.

Frequency character methods compare changes in the frequencies of individual alleles and their gain, loss, and/or fixation among taxa. The phylogenetic trees are based on minimizing the number of genetic changes between taxa. Swofford and Berlocher's (1987, 1988) Frequency parsimony (FREQPARS vers. 2.0) and Felsenstein's (1981, 1984, 1988) Continuous character—Maximum likelihood (CONTML in PHYLIP Phylogeny Inference Package vers. 3.1) methods were used.

FREQPARS generates a tree on which each allele undergoes the least amount of frequency change, while at the same time ensuring that allelic frequencies in the hypothetical ancestors add to 1.00. This program was modified for use on this particular data set by D. Swofford. CONTML models evolutionary change at a locus as a Brownian motion process without requiring the assumption of rate uniformity across

lineages. All of the clinid species and the three labrisomid species closest in genetic distance to the Clinidae (*Auchenionchus microcirrhys*, *Alloclinus holderi*, and *P. integripinnis*) were analyzed. Global branch swapping and 10 separate trials using the random-number jumble option were used in CONTML.

A discrete character parsimony analysis using Phylogenetic Analysis Using Parsimony (PAUP 3.0; Swofford, 1990) was also used, in which the loci served as the characters and fixed (frequencies = 1.00) and predominant alleles (frequencies >0.85, >0.90, and >0.95) were coded as discrete character states (in separate computer analyses; Tables 2–3). Using only fixed alleles is more acceptable to some cladists who do not regard variable characters as providing proper phylogenetic data (Crother, 1990). However, this approach has the disadvantage of discarding the information contained in allelic variation. Allelic frequencies less than the cut-off level were not coded, and, if there was not an allele with a given frequency at a particular locus, the character state data for that species were coded as missing. Exhaustive searches were employed, and trees were rooted with the labrisomid *A. microcirrhys*.

A multicharacter state parsimony analysis using PAUP 3.0 (Swofford, 1990) was also employed, in which, as above, alleles were coded as unordered character states (with multiple character states analyzed as polymorphisms) and loci as the characters (Table 3). This approach has the advantage of including allelic variation but, as in the discrete character analysis, disregards allelic frequency information. Exhaustive searches were used and trees were rooted to *A. microcirrhys*.

Phylogenetic hypotheses generated by the four programs were compared with each other and with those based on morphological data from C. Hubbs (1952), Springer (1970), Stephens and Springer (1973), George and Springer (1980), and Stepien and Rosenblatt (1991) (see characters 41–53, Table 3). Discrete morphological data were analyzed using PAUP (Swofford, 1990), using unordered character states and an exhaustive search (rooted with the cryptotremid labrisomids *Auchenionchus microcirrhys* and *Alloclinus holderi*). These morphological data were also added to the discrete and multistate data sets in separate PAUP analyses, using unordered character states and exhaustive searches (as above) and exhaustive searches

TABLE 2. GENOTYPIC DISTRIBUTIONS OF LOCI FOR CLINIDS AND LABRISOMIDS.

Locus	Number of specimens of each genotype per species (and relative allelic mobilities ¹)				
	<i>Myxodes viridis</i>	<i>Heteroclinus whiteleggi</i>	<i>Auchenionchus microcirrhus</i>	<i>Alloclinus holderi</i>	<i>Paracrinus integripinnis</i>
sAat-A	bb(090):32 ab(100):01	bb(090):09	aa(100):04	bb(090):10	bb(090):21
sAat-B	aa(100):39	aa(100):10	cc(095):04	cc(095):43	cc(095):42
mAat-A	aa(100):25	aa(100):08 ab(200):01	aa(100):04	aa(100):60	aa(100):21
sAcoh-A	ee(115):40	dd(075):04	cc(105):04	aa(100):38 ad(075):04	ff(125):18
Acp-I	aa(100):22	aa(100):09	cc(140):04	bb(115):10 bc(140):01	bb(115):21
Acp-A	cc(090):36	cc(090):09	cc(090):04	ee(135):10 ef(155):03	hh(120):12 eh(135):04
Adh-A	aa(100):32	aa(100):07	aa(100):04	bb(090):31	aa(100):12
Adh-B	aa(100):30	aa(100):08	bb(050):03 bc(070):01	aa(100):30 ac(070):05	aa(100):12 ac(070):02
Ak-A	bb(200):42	bb(200):16	bb(200):04	bb(200):45	bb(200):20 bc(230):01
Ck-A	bb(115):44	bb(115):09	cc(105):04	cc(105):42	cc(105):21
Ck-B	bb(105):41	cc(095):09	aa(100):04	aa(100):37 ab(105):01	bb(105):13
Ck-C	bb(117):42	bb(117):09	cc(125):04	cc(125):07 cd(140):01	dd(140):13
Est-1	cc(090):11 ac(100):01	bb(110):08 ab(100):01	dd(120):04	aa(100):08	aa(100):07
Est-2	bb(090):11	cc(110):09	cc(110):04	cc(110):09	dd(150):07
Est-3	bb(090):20	bb(090):09	dd(110):04	cc(105):42	dd(085):12
Fumh-A	bb(120):33 ab(100):02	bb(120):09	aa(100):04	aa(100):09 ac(150):03	bb(120):20
G6pdh-1	bb(120):42	bb(120):14	bb(120):04	bb(120):10	bb(120):10 be(130):02
G6pdh-2	cc(090):37 bc(110):02	bb(110):08 bd(080):01	ee(120):04 ef(090):02	ee(120):10	ee(120):10
Gpi-A	dd(070):26	aa(100):10	aa(100):03 ae(115):01	dd(070):40 df(115):03	aa(100):18 ad(070):02
Gpi-B	bb(115):11	aa(100):04	aa(100):04	dd(200):35 df(215):05	ee(065):30
Gtdh-A	aa(100):42 ac(075):01	bb(110):09	bb(110):04	bb(110):24	bb(110):20
Gapdh-A	aa(100):43	aa(100):09	cc(200):03 bc(120):01	cc(200):45	dd(080):21 ad(100):02
Gapdh-C	aa(100):42 ab(120):01	bb(120):10	bb(120):04	bb(120):40	bb(120):20
G3pdh-B	ee(120):27	bb(080):14	ff(060):03 af(100):01	ff(060):42	gg(115):07 gf(060):01
Iddh-A	bb(060):08 ab(100):01	cc(125):04	cc(125):04	dd(200):20 de(105):02	ee(106):06 ce(125):02
sIdh-A	cc(095):39	bb(115):09	bb(115):04	bb(115):42	bb(115):05 bc(095):02
mIdh-A	dd(110):40	cc(120):07	cc(120):04	cc(120):25	cc(120):14
Ldh-A	dd(080):43	aa(100):05 ac(090):01	aa(100):04	aa(100):45	ee(120):10
Ldh-B	cc(105):42	aa(100):07	aa(100):04	aa(100):32	aa(100):12
Ldh-C	aa(100):24	aa(100):08	aa(100):04	aa(100):45	aa(100):12

TABLE 2. CONTINUED.

Locus	Number of specimens of each genotype per species (and relative allelic mobilities ¹)				
	<i>Myxodes viridis</i>	<i>Heteroclinus whiteleggei</i>	<i>Auchenionchus microcirrhus</i>	<i>Alloclinus holderi</i>	<i>Paraclinus integripinnis</i>
sMdh-A	aa(100):42	cc(110):14 ac(100):01	bb(070):02 ab(100):02	aa(100):10	ee(095):06
sMdh-B	dd(110):30 bd(090):03	bb(090):07 be(070):01	ff(060):04	cc(080):40	gg(105):10
Mpi-A	aa(100):31	aa(100):04	bb(085):04	cc(120):05 ac(100):03	cc(120):05
Pep-A	dd(080):44	aa(100):13 ad(080):01	ee(115):03 de(080):01	dd(080):25 ad(100):03	dd(080):03 df(085):03
Pep-B	cc(095):30	bb(120):12	bb(120):04	cc(095):40 cd(110):05	aa(100):22 ad(110):02
Pep-3	cc(050):28 cd(080):01	bb(125):12 bc(050):02	bb(125):04	bb(125):40	ee(035):07 ef(070):02
Pgm-A	cc(070):41	bb(110):06 bd(050):01	bb(110):04	ee(080):39 ef(060):03	ee(080):20
Pgdh-A	cc(120):37	dd(080):10	cc(120):04	cc(120):45	cc(120):21
sSod-A	dd(030):41	ee(120):06	ff(060):04	ee(120):40 eg(145):10	hh(110):19 fh(050):01
Xdh-A	cc(080):40 ac(100):01	bb(110):09	cc(080):04	cc(080):20	bb(110):08 bc(080):02

* Relative allelic mobilities were measured against the standard of the most common allele in the population of *Gibbonsia elegans* from La Jolla, California (see Materials and Methods).
For heterozygotes, the relative allelic mobility of the rarer allele is given in parentheses.

(Table 3). Strict (Rohlf, 1982), Adams (1972, 1986), and 50% majority rule (Rohlf, 1982) consensus trees were run on the shortest trees from the discrete and multistate PAUP analyses, and 1000 bootstrap replications (Felsenstein, 1985) on the data sets were performed using the branch-and-bound algorithm (Hendy and Penny, 1982). Consistency indices (C.I.; Swofford, 1990), g-1 skewness statistics (Sokal and Rohlf, 1981; Hillis, 1991; Huselsenbeck, 1991), and lengths of most parsimonious trees are reported for all PAUP analyses. The g-1 statistic measures degree of skewness of tree length distributions, providing a test of the relative strength of the phylogenetic signal (Hillis, 1991; Huselsenbeck, 1991).

RESULTS

Allozyme data for 40 presumptive gene loci from the clinids *H. rostratus*, *G. elegans*, *G. metzi*, and *G. montereyensis* are given in Stepien and Rosenblatt (1991) and those for *M. viridis*, *H. whiteleggei*, and the labrisomids *Auchenionchus microcirrhus*, *Alloclinus holderi*, and *P. integripinnis* are summarized in Table 2. Allozyme data for

the chaenopsids and remaining labrisomids are given in Stepien et al. (1992). Zymograms illustrating similarities and differences between taxa are given in Figure 2. Genetic distances for all individual population samples of the North American clinid taxa are presented and analyzed in Stepien and Rosenblatt (1991). Populations sampled in Stepien and Rosenblatt (1991) were in Hardy-Weinberg equilibrium and were thus pooled in the present study.

All methods of analysis of allozyme data, including frequency character, genetic distance, discrete character, and multistate character parsimony approaches yielded one or both of two most parsimonious trees. These two trees were identical except among relationships within the genus *Gibbonsia* (Fig. 3) and were obtained when the trees were rooted with different species of labrisomids and chaenopsids.

The two most parsimonious phylogenetic trees obtained from the various types of data analyses are presented in Figure 3A–B. Branches and nodes are lettered, and allozyme character state synapomorphies and autapomorphies delineating taxa at each of these, for both trees, are given in Tables 4 and 5. Possible homoplasies

TABLE 3. DATA MATRIX FOR PAUP ANALYSES, INCLUDING ALLOZYME (CHARACTERS 1-40) AND MORPHOLOGICAL CHARACTERS (41-53).

Taxa	Presumptive gene locus									
	sAat-A 1	sAat-B 2	mAat-A 3	sAat-A 4	Acpi-1 5	Acpi-A 6	Adh-A 7	Adh-B 8	Ak-A 9	Ck-A 10
<i>H. rostratus</i>	a	a***,b,c	b	b*,a	b	b**,a,c	b*,a	a	b	b
<i>G. elegans</i>	a	a***,b	a	a**,b,c	a	a***,d	a***,b	a	a	a
<i>G. metzi</i>	a	a	b	a**,b,f	b	a***,d	a	a	a	a
<i>G. montereyensis</i>	a	b	b	a*,b	a	a*,d	a	a	a	a
<i>M. viridis</i>	b***,a	a	a	e	a	c	a	a	b	b
<i>H. whiteleggei</i>	b	a	a***,b	d	a	c	a	a	b	b
<i>A. microcirrhys</i>	a	c	a	c	c	c	a	b***,c	b	c
<i>H. rostratus</i>	a	a	b	b	a	b	a	a	a	a
<i>G. elegans</i>	a	a	a	a***,b,c	a	a,b	a	a***,b,c,d	a	a
<i>G. metzi</i>	a	a	a	a**,b,c	a	b***,a	a	a	a	a
<i>G. montereyensis</i>	a	b	a	a***,b	a	b***,a	a	a***,b,c,d	a	a
<i>M. viridis</i>	b	b	b	b	a*,b	b***,a	a	e	b	b
<i>H. whiteleggei</i>	c	b	c	b	b	b	a	c	b	b
<i>A. microcirrhys</i>	a	c	c	d	b	a	b*,c	f**,a	b	b
<i>H. rostratus</i>	a	a	a** ,b	a	b** ,a	a	a	b***,a	b*,a	a
<i>G. elegans</i>	a	a	a** ,b,c,d	a*** ,c	a	a	a	a	a	a
<i>G. metzi</i>	a	a	a** ,b,c	a*** ,c	a	b	a	a	a	a
<i>G. montereyensis</i>	a	a	a	a*** ,c	a	b***,a	a	a	a	a
<i>M. viridis</i>	c** ,b	a	d	b	c	d	b** ,a	d	c	a
<i>H. whiteleggei</i>	b* ,d	b	a	a	b	c	c	a** ,c	a	a
<i>A. microcirrhys</i>	e* ,f	b	a* ,e	a	b	c	c	a	a	a
<i>H. rostratus</i>	a	a* ,b	a	c** ,a	b	b	b** ,a	b	a	a
<i>G. elegans</i>	a	a** ,b,c	a	a*** ,b	a	a	a***,b	a	a** ,c,e	a
<i>G. metzi</i>	a	a** ,b,d	a	b	a	b***,a	b***,a	a	a***,c	a
<i>G. montereyensis</i>	b** ,a	a***,b	a	a	d** ,a	b	b	a	a** ,c	a
<i>M. viridis</i>	c* ,a	d* ,b	a	d	c	c	c	c	d	c***,a
<i>H. whiteleggei</i>	a	b** ,e	a	a** ,d	b	b***,c	b** ,d	e	b	b
<i>A. microcirrhys</i>	b? ,a	f	b	e* ,d	b	b	b	f	c	c

TABLE 3. CONTINUED.

Taxa	Morphological characters (see key below)												
	41	42	43	44	45	46	47	48	49	50	51	52	53
<i>H. rostratus</i>	b	b	b	a	a	b	b	a	a	a	a	b	b
<i>G. elegans</i>	b	b	b	a	a	b	b	b	b	a	b	c	b
<i>G. metzi</i>	b	b	b	a	a	b	b	a	a	a	b	c	b
<i>G. montereyensis</i>	b	b	b	a	a	b	b	b	b	a	b	c	b
<i>M. viridis</i>	b	b	b	a	a	b	a	a	a	b	b	b	b
<i>H. whiteleggeri</i>	b	b	b	b	b	?	a	a	a	a	a	a	a
<i>A. microcirrhus</i>	a	a	a	a	a	a	a	a	a	a	a	a	a

In discrete character state analyses, only the most common allele (the first listed) was used. ? = frequency of most common allele < 85% (in discrete analyses) or character state unknown (for morphological data).

* = frequency of most common allele < 90%.

** = frequency of most common allele < 95%.

*** = frequency of most common allele < 100%.

In multicharacter state analyses, all alleles were coded as character states.

Key to morphological characters

41. Cordlike ligament connecting ceratohyal and dentary symphysis (George and Springer, 1980). a = absent, b = present
42. Scales absent or with radii on anterior margins only (a), scales with radii on all margins (b) (C. Hubbs, 1952; George and Springer, 1980).
43. Occur in red, green, and brown color morphs which match color of plant backgrounds (C. Hubbs, 1952; Penrith, 1969; Stepien, 1990). a = absent, b = present.
44. Male intramittent organ (C. Hubbs, 1952; Penrith, 1969; George and Springer, 1980). a = absent, b = present.
45. Trophodermic matrotrophy (ovoviviparity; C. Hubbs, 1952; Penrith, 1969; George and Springer, 1980). a = absent, b = present.
46. Depth segregation of adult males and adult females; males living deeper than females (Stepien 1987, 1990; Stepien et al., 1988). a = absent, b = present.
47. Size sexual dimorphism; adult females larger in size than adult males at given ages (Stepien 1987, 1990; Stepien et al., 1988). a = absent, b = present.
48. Unequal spacing of posterior soft dorsal fin rays (C. Hubbs, 1952). a = absent, b = present.
49. Two or more dorsal ocelli above lateral line (C. Hubbs, 1952; Stepien and Rosenblatt, 1991). a = absent, b = present.
50. Vomerine teeth (Springer, 1970). a = present, b = absent.
51. Palatine teeth (Springer, 1970). a = present, b = absent.
52. Last dorsal fin ray; a = bound for complete length to caudal peduncle, b = free from caudal peduncle, c = tip only free from caudal peduncle (C. Hubbs, 1952; Springer, 1970).
53. Deep notch between dorsal spines 3 and 4 (C. Hubbs, 1952; Springer, 1970). a = absent, b = present.

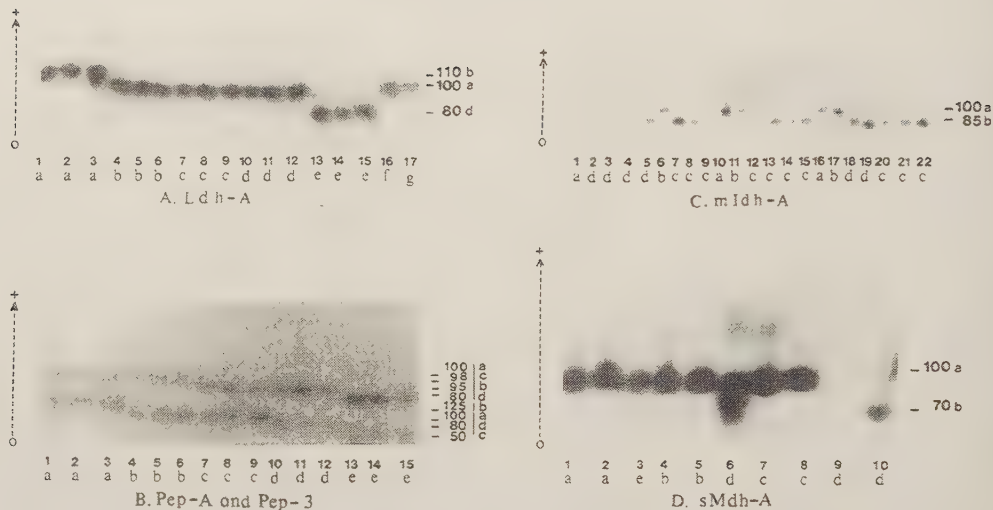


Fig. 2. Examples of zymograms of isozyme expressions from tissue extracts from clinid and labrisomid taxa. o = origin of gel. Taxa are lettered as follows: a = *Heterostichus rostratus*, b = *Gibbonsia elegans*, c = *Gibbonsia metzi*, d = *Gibbonsia montereyensis*, e = *Myxodes viridis*, f = *Heteroclinus whiteleggi*, and g = *Auchenionchus microcirrhus*. Other loci are visible on some of the photographs, e.g., sldh-A on gel C and sMdh-B on gel D. Heterozygotes include gel A, fish 3-a, alleles a/b; gel B, Pep-A (top bands), fish 12-d, alleles b/d; Pep-3 (lower bands), fish 13-e, alleles d/c; and gel D, fish 6-d, alleles a/b.

of the two trees are compared in Table 5. Morphological synapomorphies at each branch are summarized in Table 3 and the Discussion.

Goodness-of-fit statistics for the Wagner distance tree varied with the number of taxa included (number of labrisomid tribes and inclusion of the Chaenopsidae). Cophenetic correlation (Swofford and Selander, 1981) values ranged from 0.87, when all 10 labrisomid species were included, to 0.93 when rooted to the two most similar labrisomid species (*Auchenionchus microcirrhus* and *Alloclinus holderi*), and 0.99 when only the eastern Pacific myxodin clinid species were analyzed. Cophenetic correlation of the three family data set (Clinidae, Labrisomidae, and Chaenopsidae) was 0.80 (Stepien et al., 1992).

The tree derived from the Wagner genetic distance method (Fig. 3B) is identical to the most parsimonious tree from the frequency character programs (Fig. 3A) in all but the last two branches (the relationships among species in the genus *Gibbonsia*). The North American clinid taxa are separated into two lineages, the genera *Gibbonsia* and *Heterostichus*.

Continuous character-Maximum likelihood

(Felsenstein, 1988), a frequency character approach, yielded a single tree (Fig. 3A) in all 10 independent analyses. *Gibbonsia elegans* is depicted as the basal clade within the genus and is the sister group to *G. montereyensis* and *G. elegans*. This tree had Ln likelihood values (Felsenstein, 1988) of 127.26.

Frequency parsimony (Swofford and Berlocher, 1988) yielded two most parsimonious trees (Fig. 3A-B), which differ in whether *G. metzi* (tree A) or *G. elegans* (tree B) is the basal clade in the genus. The lengths of these trees are 134.44 and 134.65, respectively. The next shortest tree places *G. montereyensis* as the basal clade in the genus and has a length of 136.14. The shortest tree (Fig. 3A) obtained with Frequency parsimony was thus identical to the only tree obtained with Continuous character-Maximum likelihood.

Analysis of fixed character state data (allelic frequencies = 100%) using PAUP 3.0 (Swofford, 1990) yielded three most parsimonious trees, which included each of the three species of *Gibbonsia* as sister to the other two (57 steps, C.I.s = 0.93, and g-1 skewness = -1.20 with allozyme data only and 74 steps, C.I.s = 0.91,

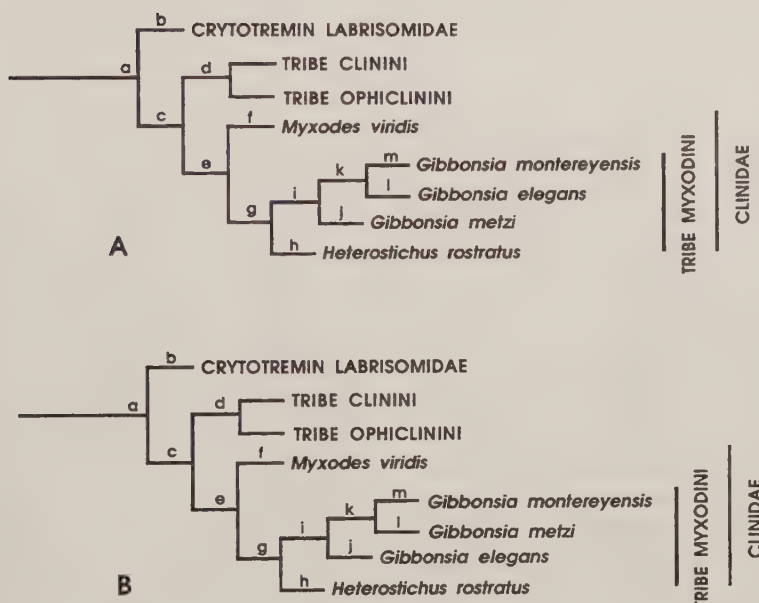


Fig. 3. Most parsimonious phylogenetic trees derived from various approaches for analyzing allozyme data, including two frequency character, one discrete character parsimony, one multicharacter state parsimony, and one genetic distance method. (A) Most parsimonious tree derived from morphological data and frequency character methods for analyzing allozyme data, including Frequency Parsimony and Continuous character-Maximum likelihood, showing relationships of the Clinidae. This tree is also one of the most parsimonious trees from the discrete character and multicharacter state parsimony analyses. (B) Tree derived from the Wagner genetic distance method. This was also the second most parsimonious tree produced by the FREQPARS analysis. This tree is also one of the most parsimonious trees from the discrete and multistate character parsimony analyses. This was the most parsimonious tree from the PAUP analysis of a combination of multicharacter state allozyme and morphological data.

and g-1 skewness = -1.28 with both allozyme and morphological data included). At the 0.95 cut-off level of allelic frequency, trees 3A and 3B were equally parsimonious (65 steps, C.I.s = 0.92, and g-1 skewness = -1.12 with allozyme data only and 82 steps, C.I.s = 0.90, and g-1 skewness = -1.16 with both allozyme and morphological data). At the 0.90 cut-off level, tree 3B was the most parsimonious (78 steps, C.I. = 0.89, and g-1 skewness = -0.92 with allozyme data only and 95 steps, C.I. = 0.91, and g-1 skewness = -0.98 with both allozyme and morphological data). Tree 3B was also the most parsimonious at the 0.85 cut-off level (85 steps, C.I. = 0.93, and g-1 skewness = -0.79 with allozyme data only and 102 steps, C.I. = 0.91, and g-1 skewness = -0.87 with inclusion of morphological data).

Discrete morphological characters for these

taxa (characters 41–53 of Table 3) were also analyzed separately using PAUP. Two equally parsimonious trees were obtained (15 steps, C.I.s = 0.93, g-1 skewness = -1.12)—tree 3A and a tree with the positions of *H. rostratus* and *M. viridis* reversed. A bootstrapping consensus tree using branch-and-bound (Hendy and Penny, 1982), 50% majority-rule, and 1000 replications resulted in confidence intervals of 92% for node “e” (of Fig. 3A), 45% for node “g,” 68% for node “i,” and 87% for node “k.”

Multistate character PAUP analysis of allozyme data (see Table 3) resulted in three most parsimonious trees, as in the 100% fixed discrete analysis (63 steps, C.I.s = 0.92, g-1 skewness = -0.95). Bootstrapping with branch-and-bound (Hendy and Penny, 1982), 80% majority-rule, and 1000 replications yielded confidence intervals (Felsenstein, 1985) of 98% for

TABLE 4. ALLOZYME CHARACTER STATES LINKING AND DISTINGUISHING TAXA AT BRANCHES AND NODES A THROUGH F OF TREES SHOWN IN FIGURE 3A-B.

Branch or node					
a	b	c	d	e	f
sAat-A(a)	sAat-B(c)	sAat-A(b)	*sAat-A(a)	Est-2(b)	mAat-A(b)
mAat-A(a)	Acp-1(c)	sAat-B(a)	sAcoh-A(d)	*Est-2(c)	sAcoh-A(e)
Acp-A(c)	Adh-B(b)	mAat-A(b)	*Ck-B(a)	Gadph-C(a)	*Ck-B(a)
Adh-A(a)	Adh-B(c)	Acp-1(a)	Ck-B(c)	Gtdh-A(a)	Ck-B(b)
Ak-A(b)	sAcoh-A(c)	Adh-B(a)	Est-1(b)	*Gtdh-A(b)	Est-1(c)
Ck-B(a)	Ck-A(c)	Ck-A(b)	*Fumh-A(a)	Gpi-A(d)	*G3pdh-B(a)
Est-2(c)	Ck-C(c)	Ck-C(b)	*G3pdh-B(a)	*mIdh-A(c)	G3pdh-B(e)
Fumh-A(a)	Est-1(d)	Est-1(a)	G3pdh-B(c)	Iddh-A(a)	G6pdh-2(c)
Gapdh-C(b)	Est-3(d)	Est-3(b)	G6pdh-2(d)	*Iddh-A(c)	Gtdh-A(c)
G3pdh-B(a)	Gapdh-A(b)	Fumh-A(b)	Ldh-A(c)	Ldh-A(d)	*Gpi-A(a)
G6pdh-1(b)	Gapdh-A(c)	Gapdh-A(a)	sMdh-A(c)	sMdh-B(d)	Gpi-A(d)
Gtdh-A(b)	G3pdh-B(f)	G6pdh-2(b)	sMdh-B(e)	*Pep-A(d)	*Gpi-B(a)
Gpi-A(a)	G6pdh-2(e)	sMdh-B(b)	*Pep-A(a)	Pep-B(c)	Gpi-B(b)
Gpi-B(a)	G6pdh-2(f)	Mpi-A(a)	*Pgdh-A(c)	Xdh-A(a)	*sIdh-A(b)
sIdh-A(b)	Gpi-A(e)	Pep-A(a)	Pgdh-A(d)		sIdh-A(c)
mIdh-A(c)	sMdh-A(b)	Pep-3(c)	Pgm-A(d)		mIdh-A(d)
Iddh-A(c)	sMdh-B(f)		sSod-A(e)		Iddh-A(b)
Ldh-A(a)	Mpi-A(b)		Xdh-A(b)		*Ldh-A(a)
Ldh-B(a)	Pep-A(e)		*Xdh-A(c)		Ldh-A(d)
Ldh-C(a)	sSod-A(f)				*Ldh-B(a)
sMdh-A(a)					Ldh-B(c)
Pep-A(d)					*Pep-A(a)
Pep-B(b)					*Pep-B(b)
Pep-3(b)					*Pep-3(b)
Pgdh-A(c)					Pep-3(d)
Pgm-A(b)					*Pgm-A(b)
Xdh-A(c)					Pgm-A(c)
					sSod-A(d)

* = Character state losses.

node "e," 92% for node "g," and 87% for node "i" (of trees in Fig. 3). Tree 3B was the most parsimonious obtained with a combination of morphological and multistate allozyme data (characters 1-53 of Table 3; 102 steps, C.I. = 0.91, g-1 skewness = -0.87). Bootstrapping with branch-and-bound (Hendy and Penny, 1982), 80% majority-rule, and 1000 replications yielded confidence intervals (Felsenstein, 1985) of 99% for node "e," 99% for node "g," and 92% for node "i" (of trees in Fig. 3).

In all PAUP analyses, strict (Rohlf, 1982), Adams' (1972, 1986), and 50% majority-rule (Rohlf, 1982) consensus analyses of the shortest trees yielded unresolved trichotomies for the genus *Gibbonsia*. Allozyme character state synapomorphies linking taxa at the branches of the two trees are compared in Tables 4 and 5, which show that trees 3A and 3B are supported by equal numbers of total synapomorphies at nodes

"g," "i," and "k" (18 vs 16 at node "g," 15 vs. 16 at node "i," and 1 vs 2 at node "k"). Tree 3A has six apparent homoplasies and 67 character state losses, and tree 3B has five apparent homoplasies and 68 character state losses, listed in Table 5.

DISCUSSION

Four different approaches for the phylogenetic analysis of allozyme data yielded parsimonious relationships that were identical, except within the genus *Gibbonsia* (Fig. 3). This set of phylogenetic hypotheses is further supported by the known morphological characters distinguishing these taxa and largely corroborates the relationships proposed by C. Hubbs (1952), Penrith (1969), Springer (1970), and George and Springer (1980). Analysis of allozymes yielded a large data set that provided an

TABLE 5. ALLOZYME CHARACTER STATES LINKING AND DISTINGUISHING TAXA AT BRANCHES AND NODES G THROUGH M OF TREES SHOWN IN FIGURE 3A VERSUS 3B.

g	h	i	j	k	l	m
Tree A						
*sAat-A(b)	xsAat-B(c)	*Acp-A(c)	*sAat-B(b)	*Acp-1(b)	xmAat-A(a)	*sAat-B(a)
sAat-B(b)	*Acp-1(a)	Acp-A(d)	*Acp-1(a)	xG3pdh-B(c)	*mAat-A(b)	*Adh-A(b)
*mAat-A(a)	Acp-A(b)	Ak-A(a)	sAcoh-A(f)	G3pdh-B(d)	sAcoh-A(c)	*Ck-C(a)
sAcoh-A(a)	*Ck-C(b)	*Ak-A(b)	*Adh-A(b)	*Mdh-B(d)	*Ck-C(b)	*Est-3(c)
sAcoh-A(b)	Fuhm-A(a)	Ck-A(a)	*Ck-C(a)	*Pep-B(b)	*mIdh-A(b)	*Gpi-A(b)
Acp-1(b)	*G3pdh-B(b)	*Ck-A(b)	*G3pdh-B(b)	*Pgm-A(b)	xGpi-A(d)	*Gpi-A(c)
Acp-A(a)	*Gpi-A(d)	Est-2(a)	Gpi-A(b)		sMdh-B(c)	xMdh-A(b)
Acp-A(b)	Ldh-A(b)	*Est-2(b)	*mIdh-A(a)		*Pep-B(c)	*Pep-A(a)
Adh-A(b)	Ldh-B(b)	Est-3(a)	*Pep-A(a)		xsSod-A(e)	*Pep-B(a)
Ck-C(a)	*sMdh-B(d)	Est-3(c)				xPep-3(d)
Gapdh-C(a)	Pep-A(c)	Gpi-A(c)				*Pgdh-A(b)
*Gapdh-C(b)	*Pep-B(c)	Gpi-B(c)				
G6pdh-1(a)	sSod-A(b)	mIdh-A(b)				
*G6pdh-1(b)		*sIdh-A(b)				
G6pdh-2(a)		Pep-A(b)				
*G6pdh-2(b)		Pep-B(a)				
Gpi-A(b)		Pep-3(a)				
sIdh-A(a)		*Pep-3(b)				
mIdh-A(a)		Pgm-A(a)				
sMdh-B(a)		sSod-A(a)				
*Pep-A(d)		sSod-A(c)				
*Pep-3(c)						
Pgdh-A(a)						
Pgdh-A(b)						
Pgdh-A(c)						
*Xdh-A(c)						
Tree B						
*sAat-A(b)	xsAat-B(c)	*Acp-A(c)	*mAat-A(a)	*mAat-A(a)	*sAat-B(b)	*sAat-B(a)
sAat-B(b)	*mAat-A(a)	Acp-A(d)	sAcoh-A(c)	*Adh-A(b)	sAcoh-A(f)	*sAcoh-A(c)
sAcoh-A(a)	*Acp-1(a)	Ak-A(a)	*Acp-1(b)	*Ck-C(a)	*Acp-1(a)	*Acp-1(b)
sAcoh-A(b)	Acp-A(b)	*Ak-A(b)	*Ck-C(b)	Gpi-A(d)	*G3pdh-B(b)	*Est-3(c)
Acp-1(b)	*Ck-C(b)	Ck-A(a)	sMdh-B(c)	mIdh-A(b)	*G3pdh-B(c)	*Gpi-A(b)
Acp-A(a)	*Fumh-A(a)	*Ck-A(b)	*sMdh-B(d)	*Pep-A(a)	*G3pdh-B(d)	*Gpi-A(c)
Adh-A(b)	*G3pdh-B(b)	Est-2(a)	*Pep-B(b)		*mIdh-A(a)	xsMdh-A(b)
Ck-C(a)	*Gpi-A(d)	*Est-2(b)	*Pep-B(c)			*sMdh-B(d)
Gapdh-C(a)	Ldh-A(b)	Est-3(a)	*Pgm-A(b)			*Pep-B(a)
*Gapdh-C(b)	Ldh-B*b	Est-3(c)	xsSod-A(e)			*Pep-B(b)
G6pdh-1(a)	*Mdh-B(d)	G3pdh-B(b)				xPep-3(d)
*G6pdh-1(b)	*Pep-A(a)	xG3pdh-B(c)				*Pgdh-A(b)
G6pdh-2(a)	Pep-A(c)	G3pdh-B(d)				*Pgm-A(b)
*G6pdh-2(b)	*Pep-B(c)	Gpi-A(c)				
Gpi-A(b)	sSod-A(b)	Gpi-B(c)				
sIdh-A(a)		*sIdh-A(b)				
mIdh-A(a)		Pep-A(b)				
sMdh-B(a)		Pep-B(a)				
*Pep-A(d)		Pep-3(a)				
*Pep-3(c)		*Pep-3(b)				
Pgdh-A(a)		Pgm-A(a)				
Pgdh-A(b)		sSod-A(a)				
*Pgdh-A(c)		sSod-A(c)				
*Xdh-A(c)						

* = Character state losses. x = Possible homoplasy of electromorphs with the same net electric charge.

independent test for the identification of synapomorphies and monophyletic relationships among the Clinidae.

The family Labrisomidae, which was tested as the sister group in the present study, was recently distinguished from the Clinidae by George and Springer (1980). Labrisomids are widely distributed throughout the New World tropics and are also represented by two species in the eastern Atlantic, on the coast of Africa (Nelson, 1984; see Fig. 1B). They are distinguished from the Clinidae by a few morphological characters (see Introduction), and results of the present study support their familial separation.

Results of the present study suggest that the cryptotremid labrisomids, including the South American *Auchenionchus microcirrhis* and the North American *Alloclinus holderi* are sister to the Clinidae (Table 3) and indicate that the Labrisomidae may be paraphyletic (Stepien et al., 1992). In the present study, the cryptotremid labrisomid *Auchenionchus microcirrhis* and clinids share 27 allozyme character state synapomorphies, listed in Table 4. DNA sequence data from nuclear ribosomal and mitochondrial DNA from additional blennioid families and tribes (including the labrisomid tribes) are being used to further elucidate these relationships (Stepien et al., 1992; Stepien, unpubl.).

Allozyme data from the clinid species analyzed in the present study support Springer's hypothesis (Springer, 1970; George and Springer, 1980) that the Clinidae is monophyletic. Ribosomal DNA sequence data from the clinid tribes Clinini and Myxodini and the families Labrisomidae, Chaenopsidae, Tripterygiidae, and Blenniidae also support monophyly of the Clinidae (Stepien et al., 1992). The present study identifies 16 allozyme character state synapomorphies that unite the clinids examined (see branch "c" of Fig. 3A and Table 4). In addition to the morphological synapomorphies previously mentioned (see Introduction and characters 41 and 42 of Table 3), all clinids whose color patterns have been described share similar variable patterns, unlike most labrisomids (*E. asper*, however, occurs in red and green morphs; C. Hubbs, 1952). These clinids are capable of slow, extensive color changes with background (character 43, Table 3), which involve gain and loss of carotenoid pigments, and often occur in red, green, and brown morphs that match their plant habitats (Stepien 1986a, 1987, 1990; Stepien et al., 1988).

The subfamily Clininae (tribes Clinini and Ophiclinini; C. Hubbs, 1952) is distinguished from the tribe Myxodini by the synapomorphies of matritrophy and a male intromittent organ (characters 44 and 45 in Table 3). Present-day distributions of the matritrophic tribes and the Myxodini do not overlap (Fig. 1A). The present study supports the monophyly of each group and the hypothesis that they have long been separated, proposed by C. Hubbs (1952) and Penrith (1969).

Myxodins examined in the present study share nine allozyme character state synapomorphies (node "e" of Fig. 3 and Table 4). Sister relationships of the North and South American Myxodini suggest that they may have shared a continuous ancestral distribution, extending through the tropics and were later separated by the formation of a barrier to dispersal and gene flow, which led to genetic divergence (a vicariant hypothesis; see Humphries and Parenti, 1987). A vicariant event which may explain this antitropical pattern of relationship and distribution is the Miocene warming of the tropics proposed by White (1986) in his analysis of the silverside fish subfamily Atherinopsinae. Alternatively, such antitropical relationships have traditionally been explained by long-distance dispersal (C. L. Hubbs, 1952).

Briggs' (1974, 1987) competitive exclusion hypothesis offers another explanation for these antitropical biogeographic patterns. He regards antitropically distributed taxa as older, relict groups which were displaced from the tropics by more recently evolved and competitively superior species (Briggs, 1974, 1987; Newman and Foster, 1987).

Myxodes viridis and the North American myxodins share the behavioral synapomorphy of depth segregation of mature males and females, males being found deeper (character 46 of Table 3; Williams, 1954; Stepien, 1987; Stepien et al., 1988). The North American Myxodini are united by 16 allozyme character state synapomorphies and are unequivocally demonstrated to be a monophyletic clade, as all species and subspecies were analyzed in the present study (node "g" of Fig. 3 and Table 5). Unlike *M. viridis* (Stepien, 1990), the North American species share the synapomorphies of sexual differences in size, adult females attaining greater lengths than adult males (character 47 of Table 3; Stepien, 1986b, 1987; Stepien et al., 1988).

Heterostichus rostratus is distinguished from the other northern myxodins by the morphological

apomorphies of a pointed snout and a forked caudal fin, in addition to five allozyme character state apomorphies (Table 5). The genus *Gibbonsia* is a monophyletic clade defined by a suite of 15 allozyme character state synapomorphies (node "i" of Fig. 3 and Table 5). Its reduced dorsal and anal fin and vertebral elements are morphological synapomorphies further distinguishing it from *Heterostichus*.

The phylogeny in which *G. elegans* is the sister species of the other two species in the genus (Fig. 3B) contains one less apparent allozyme character state homoplasy than the tree depicting *G. metzi* as the basal clade (Fig. 3A; see Table 5 and Results). However, morphological characters distinguishing the species of *Gibbonsia* best support tree 3A (Table 3). *Gibbonsia montereyensis* and *G. elegans* share the apparent synapomorphies of reduced fin and vertebral counts and are smaller in total length than *G. metzi* (C. Hubbs, 1952). *Gibbonsia metzi* has relatively equally spaced posterior dorsal soft fin rays and scalation extending onto the caudal fin. This scale pattern is shared with *G. elegans*, whereas *G. montereyensis* exhibits the apomorphic condition of a naked caudal fin (C. Hubbs, 1952; Stepien and Rosenblatt, 1991). The latter two species also share the synapomorphies of unequally spaced posterior dorsal fin rays and the presence of prominent dorsal ocelli on the body (characters 48 and 49 of Table 3; C. Hubbs, 1952; Stepien and Rosenblatt, 1991).

Gibbonsia elegans and *G. montereyensis* share one allozyme character state synapomorphy at branch "k" of the tree shown in Fig. 3A. *Gibbonsia elegans* is distinguished from *G. montereyensis* by two allozyme character state apomorphies (Table 3, branch "l" of Table 5.).

Heterostichus and *Gibbonsia* have planktonic larval stages lasting approximately two months (Stepien, 1986b). The late larval stages, as well as juveniles and adults, are thigmotactic and have been known to raft long distances from shore with pieces of drift algae. They thus appear to be capable of some relatively long-distance dispersal. *Gibbonsia metzi* and *G. montereyensis* share primary distributions north of Point Conception (latitude 34.5°N), California, reappearing in northern Baja California, Mexico, in areas of nearshore cold-water upwelling (C. Hubbs, 1952; Stepien and Rosenblatt, 1991). *Heterostichus rostratus* and *G. elegans* share a common distribution, primarily south of Point Conception through central Baja California. Data from several studies indicated that the temper-

ature boundary at Point Conception is the most important geographic feature affecting the distributions of the California ichthyofauna, separating the warm-temperate Californian biogeographic province to the south from the cold-temperate Oregonian province to the north (C. L. Hubbs, 1952; Horn and Allen, 1978; Davis et al., 1981; Waples and Rosenblatt, 1987), which is also shown in clinid distributions (Stepien and Rosenblatt, 1991; Stepien et al., 1992).

The three species of *Gibbonsia* have been shown to differ significantly in temperature tolerances (Davis, 1974, 1977), which appears to be directly related to their present-day ranges. Although *G. montereyensis* and *G. metzi* appear capable of dispersal and a considerable degree of gene flow between populations north of Point Conception, California, and off Baja California, Mexico, has been shown (Stepien and Rosenblatt, 1991), these species are restricted to cooler waters throughout their ranges. Davis (1974, 1977) found that *G. metzi* has the widest temperature tolerance of the three species but has a lower critical thermal maximum than *G. elegans*. *Gibbonsia elegans* is more tolerant of the warmer temperatures characteristic of its present-day range and least tolerant of cooler temperatures.

Speciation in the North American Myxodini may be related to shifts in coastal temperatures during the Pliocene and early Pleistocene, which may have served as vicariant events. In the hypothesized relationships shown in the tree in Figure 3A, the first event may have separated the ancestral North American clinid stock into two groups: *Heterostichus rostratus* subtidally in the warmer waters south of Point Conception, California, and *G. metzi* intertidally to the north. A second temperature-related event may have resulted in another north/south separation of ancestral *Gibbonsia*, *G. elegans* in southern waters and *G. montereyensis* in the northern waters.

Variation in coastal current and temperature patterns may maintain gene flow between populations semi-isolated by temperature barriers (Stepien and Rosenblatt, 1991). There is strong support for dispersal and gene flow between widely separated populations of clinids, which are apparently due to their relatively long larval period, although some clinal variation is also evident. Significant differences in temperature tolerances between the species of *Gibbonsia* (Davis, 1977) and the reappearance of northern California clinids in areas of cold-water upwelling off the coast of Baja California, Mexico

(C. Hubbs, 1952; Stepien and Rosenblatt, 1991; Stepien et al., 1991), indicate that distributions of these species are determined by temperature. Also, El Niño patterns may periodically restrict the ranges of the cooler-water species (*G. metzi* and *G. montereyensis*) and expand those of the warmer-water species (*G. elegans* and *H. rostratus*). It is thus likely that speciation events in the Clinidae are related to coastal temperature patterns.

MATERIALS EXAMINED

Species used for allozyme analyses and voucher numbers.—*Heterostichus rostratus* 35 from Mission Bay, San Diego, California (SIO 90–80), 10 from Santa Catalina Island, California (SIO 90–81), 6 from Punta Clara, Baja California, Mexico (SIO 90–82), 5 from the San Benito Islands, Baja California, Mexico (SIO 90–83), and 6 from Guadalupe Island, Baja California, Mexico (SIO 90–84); *Gibbonsia elegans* 63 from Bird Rock, La Jolla, San Diego, California (SIO 90–85), 10 from Punta Clara, Baja California, Mexico (SIO 90–82), 10 from Santa Barbara, California (SIO 90–87), 3 from San Simeon, California (SIO 90–88), 10 from Middle Coronado Island, northern Baja California, Mexico (SIO 90–89), 4 from Pelican Bay, Santa Cruz Island, California (SIO 90–90), 20 from the San Benito Islands, Baja California, Mexico (SIO 90–83) and 13 from Guadalupe Island, Baja California, Mexico (SIO 90–84); *Gibbonsia metzi* 14 from Soberanes Point, Carmel, California (SIO 90–91), 55 from San Simeon, California; and 21 from Punta Clara, Baja California, Mexico (SIO 90–82); *Gibbonsia montereyensis* 10 from Soberanes Point, Carmel, California (SIO 90–82), 38 from San Simeon, California (SIO 90–88), 2 from Santa Barbara, California (SIO 90–87), 4 from middle Coronado Island, Baja California, Mexico (SIO 90–89), 18 from Punta Clara, Baja California, Mexico (SIO 90–82), and 12 from Guadalupe Island, Mexico (SIO 90–84); *Myxodes viridis* 46 from Montemar, Viña del Mar, Chile (SIO 87–132); *Heteroclinus whiteleggi* 17 from Pebble Beach, Sydney, Australia (SIO 90–158). Ten labrisomid species were employed as outgroups, including *Alloclinus holderi* 38 from Santa Catalina Island, California, 6 from the Coronado Islands, Baja California, Mexico, and 2 from La Jolla, San Diego, California (SIO 90–159); *Paraclinus integripinnis* 21 from Bird Rock, La Jolla, San Diego, California (SIO 90–157); *Auchenionchus microcirrhus* 5 from Montemar, Viña del Mar, Chile (SIO 87–139); *Paraclinus sini* 12 from San Carlos Bay, Gulf of California, Mexico (SIO 90–160); *Starksia spinipennis* 7 from the Gulf of California, Mexico; *Exerpes asper* 7 from Kino Bay in the Gulf of California, Mexico (SIO 90–160); *Labrisomus xanti* 10 from Puerto Peñasco, Mexico (SIO 90–162); *Malacotenus hubbsi* 10 from Puerto Peñasco, Gulf of California, Mexico (SIO 90–162); *Neoclinus blanchardi* 2 from La Jolla, San Diego, California (SIO 90–161) and 3 from Monterey, California, and *Mnierpes macrocephalus* 5 from Azuero Peninsula, Panama. Two species of chaenopsids were also employed as outgroups, including *Acanthemblemaria macrospilus* 4 from central Gulf of California, Mexico and *Emblemaria hypacanthus* 4 from Puerto Peñasco, Gulf of California, Mexico.

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ASSESSING EFFECTS OF UNREPLICATED PERTURBATIONS: NO SIMPLE SOLUTIONS¹

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Abstract. We address the task of determining the effects, on mean population density or other parameters, of an unreplicated perturbation, such as arises in environmental assessments and some ecosystem-level experiments. Our context is the Before-After-Control-Impact-Pairs design (BACIP): on several dates Before and After the perturbation, samples are collected simultaneously at both the Impact site and a nearby "Control."

One approach is to test whether the mean of the Impact-Control difference has changed from Before to After the perturbation. If a conventional test is used, checks of its assumptions are an important and messy part of the analysis, since BACIP data do not necessarily satisfy them. It has been suggested that these checks are not needed for randomization tests, because they are insensitive to some of these assumptions and can be adjusted to allow for others. A major aim of this paper is to refute this suggestion: there is no panacea for the difficult and messy technical problems in the analysis of data from assessments or unreplicated experiments.

We compare the randomization t test with the standard t test and the modified (Welch-Satterthwaite-Aspin) t test, which allows for unequal variances. We conclude that the randomization t test is less likely to yield valid inferences than is the Welch t test, because it requires identical distributions for small sample sizes and either equal variances or equal sample sizes for larger ones. The formal requirement of Normality is not crucial to the Welch t test.

Both parametric and randomization tests require that time and location effects be additive and that Impact-Control differences on different dates be independent. These assumptions should be tested; if they are seriously wrong, alternative analyses are needed. This will often require a long time series of data.

Finally, for assessing the importance of a perturbation, the P value of a hypothesis test is rarely as useful as an estimate of the size of the effect. Especially if effect size varies with time and conditions, flexible estimation methods with approximate answers are preferable to formally exact P values.

Key words: *environmental assessment; intervention analysis; pseudoreplication; randomization tests.*

INTRODUCTION

A common problem in basic ecological studies and applied environmental work is to determine whether a particular population, community, or other object of interest has changed after a perturbation to the environment. The answer is often obtained by conducting an experiment, consisting of a number of replicates, each randomly assigned to one of several treatments, and then applying standard statistical analyses.

However, replication with randomly assigned treatments is not always possible. In assessing the effects of

a particular power plant, we cannot randomly assign the location of the plant, or build more than one of them. Even in basic ecological work, although we can often randomly assign the perturbation to one or several of the experimental units, costs or the unavailability of replicates may make replication infeasible, particularly in whole ecosystem manipulations (Carpenter 1989, 1990, Carpenter et al. 1989).

In general, the major goal of a study of an unreplicated perturbation is to determine whether the state of the perturbed system differs significantly from what it would have been in the absence of the perturbation. Usually the "state" of the system is the mean value of some univariate or multivariate quantity, such as the population size, average size, or life history parameters

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of one or more species. We will assume the quantity of interest is univariate, e.g., the population abundance of a single species in a fixed area, although many of the general points we make also apply in the multivariate case.

Because the state of the system in the absence of the effect cannot be observed after the disturbance, we need to estimate what it would have been and compare the estimate statistically with the observed (perturbed) condition. The Before-After-Control-Impact-Pairs (BACIP) design (Stewart-Oaten et al. 1986) accomplishes this by collecting samples at both the Impact site and a nearby "Control" site. These samples are paired, in the sense that the Control and Impact sites are sampled simultaneously (as nearly as possible). Replication comes from collecting such paired samples at a number of times (dates) both Before and After the perturbation.

Each observed difference (e.g., in estimated population density) between the Impact and Control sites during the Before period is taken as an estimate of the mean difference that would have existed in the After period without the perturbation. The observed Impact-Control differences, one for each sample date, constitute a time series; we compare the differences from the Before period to those from the After period; a change in the mean difference indicates that the system at the Impact site has undergone a change relative to the Control site. The general process of estimating a change in a parameter, following a perturbation, has been termed "intervention analysis" (Box and Tiao 1975).

The BACIP design allows for natural differences between the Control and Impact locations, and for changes from the Before to the After period that influence both sites the same way (e.g., resulting from a large-scale change coincident with the putative local impact). Hypothetical examples are shown in Fig. 1.

But the design does not ensure that the assumptions of standard 2-sample tests, for comparing the "Before" set of differences to the "After" set, are satisfied. For the two-sample t test, the assumptions are:

- 1) Additivity: Time and location (site) effects are additive (i.e., in the absence of the perturbation, the expected Impact-Control difference is the same for all dates).

- 2) Independence: Observed differences from different dates are independent.

- 3) Identical Normal Distributions: The distribution of the deviation (observed difference-mean difference) is (a) the same for each time within a period; (b) the same in the After period as in the Before period; (c) Normal.

An adequate analysis must deal with these assumptions, either by supporting them (by arguing for their *a priori* plausibility and/or carrying out tests or other diagnostic procedures) or by showing that the analysis is not sensitive to their violation. This is a messy and

complicated part of the analysis, which rarely can dispel doubt altogether. Thus tests needing fewer or more plausible assumptions could be valuable.

Recently, Carpenter et al. (1989) proposed "randomized intervention analysis" (RIA), which employs a BACIP design but uses a randomization test instead of a t test to decide whether there has been a change in the difference between the impact and control sites. They argue that a "distinct advantage" of RIA is that non-Normality does not affect the test results, and imply that this solves problems of temporal trends and time lags. They add that RIA is not affected by heterogeneous variances "unlike . . . the t test," and that the effects of serial correlation will often not lead to equivocal results.

We discuss assumptions (1), (2), and (3) in reverse order, with special reference to RIA, the standard t test, and the Welch (or Welch-Satterthwaite-Aspin) modification of the t test for unequal variances (Snedecor and Cochran 1980:97). We argue: (a) RIA's robustness to non-Normality offers little advantage: the two parametric t tests are also little affected by non-Normality unless sample sizes are very small; (b) the Welch t test is approximately valid when the Before and After distributions have different variances; the other two tests are not, unless sample sizes are nearly equal; (c) the Welch t test is approximately valid when the distributions vary within a period; the others are not, although they are approximately valid if the average Before variance is nearly the same as the average After variance; (d) if the successive differences are not independent, none of the tests is valid; they may be approximately valid if the dependence is weak (and the other assumptions hold); (e) if time and location effects are not additive, none of the tests is valid; they may be approximately valid if the effects are approximately additive.

We also discuss the general application of BACIP. We argue (1) that hypothesis testing, either classical or Bayesian, is less important than estimation of the effect's size and ecological assessment of its importance, and (2) that the appropriate statistical methods will often be unavoidably messy: effects may vary with environmental conditions that can be delineated only roughly, and estimates will depend on models, which are based partly on intuition, guesswork, and mathematical convenience, and must be supported by biological arguments and formal and informal diagnostic checks.

In what follows, we assume there are n_B Before dates and n_A After dates; on the j^{th} Before date, the estimated densities were I_{Bj} at the Impact site and C_{Bj} at the Control, for a difference of D_{Bj} . Similarly we have I_{Aj} , C_{Aj} , and D_{Aj} on the j^{th} After date. The average differences are D_B and D_A . The randomization test takes the $(n_B + n_A)$ values (the D_{Bj} 's and D_{Aj} 's) as given but, under the null hypothesis, their assignment to "Before" or "After" is assumed to be random. The P value for

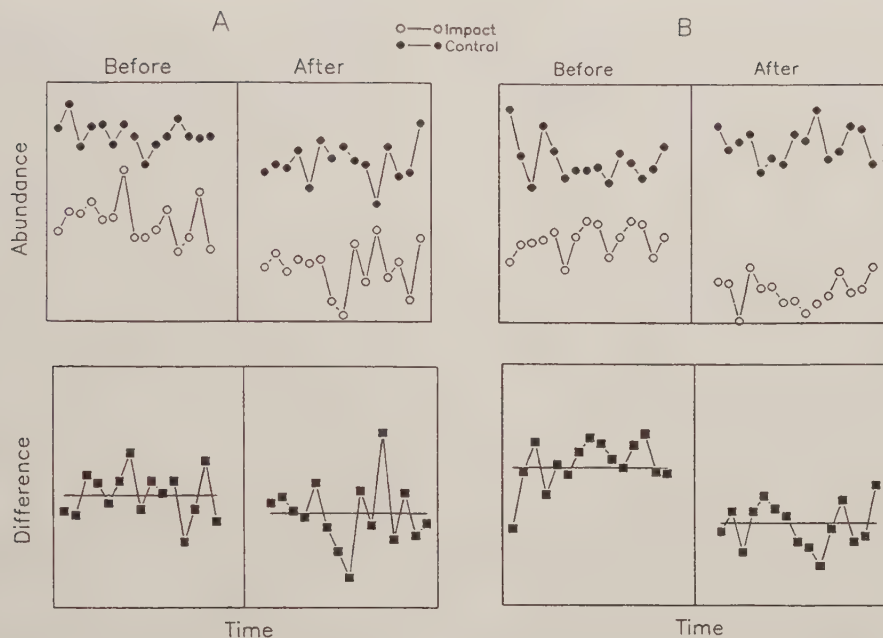


FIG. 1. Hypothetical examples of data collected using the Before-After-Control-Impact-Pairs (BACIP) design. (A) A case where average abundance is greater in the Control area than in the Impact area and where average abundance falls from Before to After. Note that the average difference between Impact and Control does not change significantly from Before to After (bottom panel), indicating that there has been no effect of the perturbation. (B) For comparison, a case where the perturbation has reduced the abundance of the species at the Impact site, leading to a decline in the difference from Before to After (bottom panel).

the test is then the fraction of the $(n_B + n_A)!/(n_B!n_A!)$ possible assignments that give a larger value of the test statistic than was actually observed (Pratt and Gibbons 1981: Chapter 6). The randomization t test uses $D_B - D_A$ (or an equivalent) as the test statistic.

IDENTICAL NORMAL DISTRIBUTIONS

It is likely that one or more of these assumptions will fail. Many biological observations are non-Normal. Even without perturbation effects, distributions may well change between periods (Before and After), e.g., due to long-term weather patterns. They may also change *within* periods, e.g., the variance of an estimate of population density may be greater in summer than in winter.

Parametric t tests

Non-normality.—Strong evidence that the standard and Welch t tests are little affected by non-Normality comes from studies of both large and small sample sizes.

For large sample sizes, it is a direct result of the Central Limit Theorem: the usual t statistics are all approximately Normal, provided only that the parent distributions have finite variances.

For small sample sizes, there are a few analytical

studies (Efron 1969, Tan 1982) providing evidence of the t test's robustness to non-Normality, but the main evidence comes from simulations, e.g., Yuen and Dixon (1973), Yuen (1974), Murphy (1976), Posten (1978, 1979), Tiku (1980), Gans (1981), Tiku and Singh (1982). Several others are reviewed by Glass et al. (1972).

A serious problem arises only from strong skewness. If D_B and D_A have different skewness, or have the same (non-zero) skewness but different variances, then $D_B - D_A$, the numerator of the t statistics, will have a skewed distribution. But such skewness is unlikely to be strong. Since I_{Bi} and C_{Bi} are estimates of similar things (e.g., population densities) based on similar sampling effort, they are likely to have similar skewness and variance: most of the skewness should cancel in the difference, $D_{Bi} = I_{Bi} - C_{Bi}$. More skewness is lost by averaging to get D_B , and still more in the difference, $D_B - D_A$, if these are similarly skewed, as is likely. If histograms of the D_{Bi} 's and D_{Aj} 's show pronounced skewness that is likely to persist through averaging and differencing, a modification of the Welch t test (Cressie and Whitford 1986) seems to solve the problem.

Distributions change between periods.—This creates little problem unless both variances and sample sizes are unequal, in which case the Welch t test is approximately valid, but the standard t test is not. The two

t statistics have the same numerator, $D_B - D_A$, which is approximately Normal by the Central Limit Theorem, except for the problem of skewness just described. Validity depends on the denominator, whose square should approximate the variance of $D_B - D_A$, with a relative error that approaches 0 as sample size increases.

The variance of $D_B - D_A$ is $S^2 = \sigma_B^2/n_B + \sigma_A^2/n_A$, where the σ^2 's are the true variances. For the Welch t test, the denominator is

$$S_W = \sqrt{[s_B^2/n_B + s_A^2/n_A]}.$$

For the standard t test, the denominator can be written as

$$S_s = \sqrt{[M_B s_B^2/n_A + M_A s_A^2/n_B]}.$$

The s^2 's are the usual variance estimates and, for $Z = A$ or B ,

$$M_Z = (1 - 1/n_Z)/[1 - 2/(n_B + n_A)].$$

As n_B and n_A approach ∞ , the s^2 's approach the σ^2 's and the M_Z 's approach 1. Thus S_W^2 does approach S^2 , but

$$S_s^2 \text{ approaches } s_B^2/n_A + s_A^2/n_B = R^2 S^2,$$

where $R^2 = (r\sigma_B^2 + \sigma_A^2)/(\sigma_B^2 + r\sigma_A^2)$ and $r = n_B/n_A$.

This shows that the Welch t test gives the correct level for large sample sizes; the simulations mentioned above verify this for moderate sample sizes. It also shows that, when its nominal level is α , the standard t test rejects the (true) null hypothesis that the Before mean is less than or equal to the After mean with probability approximately $\Phi(-Rz_\alpha)$, where Φ is the standard $N(0, 1)$ cumulative distribution function and z_α is the point for which $\Phi(-z_\alpha) = \alpha$. If either the sample sizes or the variances are approximately equal, $R \approx 1$ and the test is approximately valid. But if the smaller sample comes from the distribution with the larger variance, $R < 1$ and the test rejects more frequently than advertised. In the reverse case, it rejects less frequently.

One option is to use a test of equality of variances to decide whether to use the standard or the Welch t test. Simulations by Gans (1981) indicate that this is inferior to direct use of the Welch t test. In particular, it rejects too frequently when $R < 1$ and one variance is about half the other.

Distributions change within periods. — For this problem, some general results are given for estimates of location by Stigler (1976), for one-sample t tests by location by Stigler (1976), for one-sample t tests by Cressie and Whitford (1986). The main large sample results are similar to those just described. The numerator of both t tests, $D_B - D_A$, is approximately Normal. (There is a condition for this, roughly that the variances not be so dissimilar that most of the variability of D_B or D_A comes from a small subset of the observations; see Feller 1966:491.) Its variance is $\sigma_B^2/n_B + \sigma_A^2/n_A$, where

$\sigma_B^2 = \sum \sigma_{B_i}^2/n_B$ and $\sigma_{B_i}^2$ is the variance of the i th "Before" difference. The Welch t test is approximately valid in general, because S_W^2 approaches this variance. S_s^2 does so only if $\sigma_B^2 = \sigma_A^2$, i.e., the standard t test is valid for unequal sample sizes only if the average Before and After variances are the same.

For moderate sample sizes, the Welch t test may be "liberal": its true rejection probability may be slightly greater than the nominal value because its degrees of freedom are overestimated. The standard formula divides an estimate of $2\{E[S_W^2]\}^2$ by an estimate of $V[S_W^2]$. With heterogeneous variances, the latter estimate, $s_B^4/n_B^2(n_B - 1) + s_A^4/n_A^2(n_A - 1)$, is biased low: roughly, for Normal variables, s_B^4 approaches $(\sigma_B^2)^2$ instead of the desired $\sum \sigma_{B_i}^4/n_B = (\sigma_B^2)^2 + V(\sigma_B^2)$, where $V(\sigma_B^2)$ is the variance of the set $\sigma_{B_1}^2, \sigma_{B_2}^2, \dots$ (Cressie and Whitford 1986). But, since variances must be positive, $V(\sigma_B^2)$ is unlikely to be significantly larger than $(\sigma_B^2)^2$, which is overestimated by s_B^4 , so the correct degrees of freedom are likely to be at least half the nominal value. If the nominal value is 30 or more, this error has little effect. Unfortunately, we know of no simulation studies of this case.

Randomization tests

The assumptions for randomization tests (which are sometimes called permutation tests) are usually satisfied in experiments by the investigator's deliberate random assignment of units to treatments. This is not possible in intervention analysis: one cannot randomly assign sampling times to "Before" and "After." Instead it is assumed that "Nature" does the random assigning: under the null hypothesis, the "Before" and "After" observations are assumed to be independent draws from a common distribution.

Thus all of the assumptions listed in the *Introduction* are required, except only assumption 3(c), Normality. The user of RIA must show either that these assumptions hold or that RIA remains valid when they fail.

The randomization test is *not* valid for unequal variances. For large sample sizes, it is invalid in the same way, and to the same extent, as the standard t test discussed above. The limiting level and power of the randomization test are the same as those of the standard t test. For equal variances, this result was proved by Hoeffding (1952), with the restriction that the original distributions have finite third absolute moments, in our notation, $E|D_{B_i}|^3 < \infty$ and $E|D_{A_i}|^3 < \infty$, which is satisfied in almost all realistic cases. Romano (1990) proves it without requiring either equal variances or the third moment restriction. Our moderate sample (20 and 40) simulations with Normal variables agreed closely with these asymptotic results. One of us has also extended Hoeffding's proof to the case where variances change within periods (A. Stewart-Oaten, *unpublished manuscript*): Romano's work suggests the third moment restriction is unnecessary here, too. Romano also shows that the randomization test based on

medians is invalid for non-identical distributions, even for equal sample sizes, unless the Before and After probability densities at their medians are equal or satisfy an unlikely condition.

For small sample sizes, it is easy to construct examples for which the randomization t test is invalid for non-identical distributions, even when the variances are the same.

INDEPENDENCE

Standard two-sample tests, including t tests and randomization tests (when these are based on randomization by "Nature" rather than by an experimenter), assume that the D_{Bi} 's and D_{Ai} 's are independent.

In the assessment problem, the most likely violation is positive serial correlation: observations (D_{Bi} 's and/or D_{Ai} 's) close in time may tend to be close in value. In this case, the variance of the average of the differences, e.g., $V(D_B)$, is no longer the variance of a single observation divided by the sample size, e.g., $V(D_{Bi})/n_B$, but is larger. If this is not allowed for, all these tests will reject true null hypotheses more frequently than advertised, because observed averages will be less precise than they are assumed to be.

The observed D_{Bi} 's and D_{Ai} 's vary for two reasons. One is sampling error: the estimated Impact-Control difference at a given sampling time will not exactly equal the true difference at that time. But our concern is not with this "true difference," which itself varies naturally over time: any particular Before and After values are almost certain to be different even if there is no perturbation effect. Our concern is with the mean of the "true difference," i.e., the mean of the stochastic process of which the entire set of true differences over a period is a single realization (see Stewart-Oaten et al. 1986).

Correlation can arise from the second source of variation: the deviation between the true difference and its mean. This potential problem has been termed "pseudoreplication in time" (Hurlbert 1984). Two deviations will be correlated if the time between them is short enough that the same random events (births, deaths, movements, etc.) play significant roles in both. The variation in the true difference would then be underrepresented in the sample, leading to underestimation of the variance of D_B or D_A .

Whether serial correlation in the observed differences is sufficient to invalidate the test for an effect must be assessed by formal tests and by *a priori* arguments and models based on knowledge of the populations under study. Stewart-Oaten et al. (1986) present arguments and a simple (though easily extended) model suggesting that, provided the additivity assumption holds, only large, local events (occurring at one site but not the other) should introduce serial correlation. Non-local events (e.g., storms) should have similar population consequences at both Impact and Control, and thus cancel (at least approximately) when

we take differences. Small events (e.g., individual births and deaths) should not affect the populations for far into the future, and are likely to be swamped by the sampling errors (which are independent).

Correlation should be insignificant if sampling times are sufficiently separated so that a single event is unlikely to have a large local effect for more than one time. Arguments and models indicating how large a separation is needed should depend on the organism. For some populations, e.g., those which are short lived, highly mobile or strongly density dependent, local changes, even if large, will have only a brief effect.

For others, observations a year or more apart may be significantly correlated. A sedentary species whose larvae or seeds disperse unevenly in space over a short annual recruitment/settlement period is likely to have much the same local population within a year (between one recruitment period and the next) but quite different populations between years: variation in recruitment might be a long-lasting large local effect. Another case occurs when dispersion between Impact and Control sites is rare, as for lakes. For example, Osenberg et al. (1988) analyzed size-specific growth rates of unfish in eight lakes over a 10-yr period and found that half of the interpretable variation arose from lake X year interactions. Since the growth of these fishes is closely tied to the availability of their resources (Mittelbach 1988, Mittelbach et al. 1988, Osenberg et al. 1988, Osenberg and Mittelbach 1989), these data suggest that the abundances of the invertebrate prey also exhibit lake X year effects. Some fish populations are also known to exhibit dramatic population cycles that may result from strong age class interactions (e.g., Aass 1972, Hamrin and Persson 1986, Townsend 1989), and the timing of these cycles may well vary from lake to lake. If variation in fish density cascades to lower trophic levels (Carpenter et al. 1987), then this could introduce local year (or even longer period) effects in a number of biological variables measured in a BACIP study.

There is no guaranteed resolution of these uncertainties. Whatever testing procedure is used should be derived from a model that is plausible and survives diagnostic checking against the data, both formal tests and informal inspection, especially plots. The plausibility is important. For example, a single year of data would be insufficient for a test of serial correlation in the examples just given, since the main source of variation, between years, is never observed. An implausible model might survive diagnostic checking in these cases, and could then be used to indicate a "perturbation effect" that was really natural year-to-year variation. In most cases, we would expect several years of Before and After data to be needed, with serial correlation of the Before differences checked by the Durbin-Watson (Durbin and Watson 1971) and Ljung-Box (Ljung and Box 1978) tests, and one-way ANOVA, using years as "treatments."

If serial correlation appears significant, either *a priori*

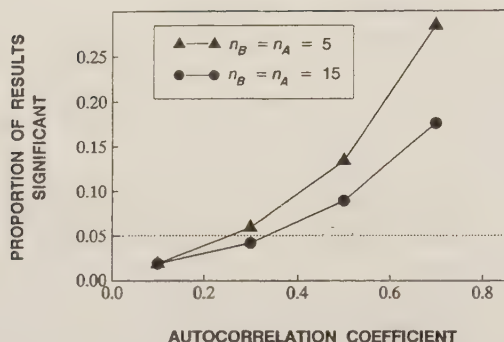


FIG. 2. An example of the effect of serial correlation on the randomization t test. The proportion of results that were significant (when H_0 is true and testing is done at the .01 level) is plotted against the value of the autocorrelation coefficient. Results are shown for sample sizes of 5 and 15 in each period. In all cases results are based on 5000 simulated trials, and randomization tests were based on the random selection of 5000 permutations. Data were generated from the same Gaussian autoregressive model of order one separately for each period.

or as a result of tests, the test for a change needs to be based on a model that includes plausible representations of the non-ignorable types of correlation (e.g., Box 1954, Box and Tiao 1965, 1975, Tiao et al. 1975, Jones 1980, 1981, McDowall et al. 1980), and is itself subjected to diagnostic checks (Box 1980).

Carpenter et al. (1989) recognize that serial correlation can inflate Type I error rates in randomization tests, but suggest that the rule "reject if the nominal P value is $< .01$ " gives a conservative .05-level test. This rule lacks generality and seems to us undesirable. First, if the correlation is weak, this test is too conservative and is inefficient. Second, if the correlation is strong enough, the test is invalid. Fig. 2 shows that, for samples of 15 from a first-order autoregressive model with equal variances, the test is invalid if $r > 0.3$.

ADDITIVITY

Suppose the two populations vary but tend to track one another so that the density in the Impact area is typically 50% of that in the Control area. Then the difference between the raw Impact and Control densities will also vary. The effects of location and time on the means at the Impact and Control sites are not additive: the time effect does not cancel when we take the differences. Such non-additivity has three consequences.

Two arise when there is systematic (e.g., seasonal) variation in the overall density. The mean Impact-Control difference (the mean of the stochastic process mentioned in the previous section) then varies over time. The correct model for the data will not be the one the test is based on, i.e., $D_{Bi} = \mu_B + \epsilon_{Bi}$ and $D_{Ai} = \mu_A + \epsilon_{Ai}$, where the errors, ϵ_i , have mean zero, but D_{Bi}

$= \mu_B + N_{Bi} + \epsilon_{Bi}$ and $D_{Ai} = \mu_A + N_{Ai} + \epsilon_{Ai}$ where the N_i 's are non-random.

One consequence is that the test for an effect is not comparing μ_B with μ_A but comparing $\mu_B + N_{B\cdot}$ with $\mu_A + N_{A\cdot}$. These could differ solely because of the choice of sampling times, e.g., if the fraction of summer samples is higher in the Before period than in the After. Of course, we can balance the samples with respect to seasons, but there may be other cycles, perhaps unknown, that are not balanced.

Second, if we have balanced cycles, the N_i 's will not bias the estimates of the means, but they will add to the estimated variances: the test will be more conservative (and less efficient) than it should be.

The third consequence arises from random natural variation, such as major storms or long spells of unusual weather. This changes densities in both areas; without additivity, it also changes their difference. Thus region-wide, long-lasting random variation may not tend to be cancelled when we take differences. The assumption that the observed differences are independent is then less plausible.

For hypothesis testing, the obvious way to satisfy the additivity assumption is to transform the data. If the data are multiplicative, as in the example above, we would expect to transform to logs. In practice, the "right" transformation may not be known, and various methods have been suggested for choosing a transformation in this situation (Tukey 1949, Box and Cox 1964, Andrews 1971, Carroll and Ruppert 1981, 1984, Hinkley and Runger 1984).

It may be that there is no monotone transformation for which the data (or the underlying process that produced them) are additive. For example, it may be that Impact densities are higher than Control in winter, but are lower in summer. In such cases a different analysis may be better. We return to this below. The main message is that the problem of non-additivity cannot be ignored, regardless of whether the final test is a t test, a randomization test, or something else.

EFFICIENCY

Validity is not the only important consideration in the choice of tests. We also want a test that is efficient, i.e., which has good power.

All three of the tests discussed here can be inefficient, because they are based on the Before and After sample averages. The average is, in some non-Normal cases, an inefficient estimator: for a given sample size, there are other unbiased estimators with much smaller variances for non-Normal distributions and only slightly larger variances for Normal distributions (Andrews et al. 1972). These "efficiency robust" estimators maintain small variances against a range of distributions by reducing the influence of the extreme observations.

A major virtue of randomization tests is the possibility of greater efficiency, from the use of robust estimates whose distributions are hard to determine, e.g.,

the median. However, as we have seen, these tests are likely to be invalid when the null distributions are not identical, as in the assessment problem.

Fortunately, there are robust estimators whose variances can be estimated. These can be used as the basis for "*t*-like" tests (both standard and Welch). Examples include trimmed means (Yuen 1974), biweight estimators (Kafadar 1982), modified maximum likelihood estimators (Tiku and Singh 1982), and many others (Andrews et al. 1972). Perhaps the easiest to use are the trimmed means, although the biweight may be the most efficient overall (Gross 1976).

In many cases a reasonable approach is to use both a Welch *t* test and an efficient Welch *t*-like test. Only if they disagree is there a problem requiring a closer look at the data. Then the focus might well be on any skewness that might cause the tests to be testing different things: if so, the investigator needs to decide what kind of change is of concern.

DISCUSSION

A main point of this paper is that there is no panacea for the difficult and messy technical problems in the analysis of data from assessments or unreplicated experiments using the BACIP design. Statistical analyses must be based on plausible models, themselves based on *a priori* empirical and theoretical arguments and checked by formal and informal methods.

In particular, randomization tests are likely to be invalid in assessment if sample sizes are unequal, because a crucial assumption, equal variances of the Before and After deviations, is likely to be violated. The Welch *t* test is more likely to be valid, because it does not require this assumption, and violation of its Normality assumption is not likely to be important to its validity. However, both tests also require the assumptions of independence and additivity.

We have concentrated on randomization *t* tests, but similar comments apply to virtually all "distribution free" and nonparametric tests. They require the additivity and independence assumptions and, contrary to frequent suggestions (e.g., Carpenter 1990, Jassby and Powell 1990), are less likely to be valid than are modifications of classical parametric tests, when distributions vary over time and sample sizes are unequal, as must be expected for assessment data.

For the remainder of this paper, we turn from the validity and efficiency of tests of "no effect" to the more important, if less technical, question of their proper role.

The "*P* value" is the probability that data indicating an effect as strongly as our data do, or more so, would arise by chance if in fact there was no effect. Reckhow (1990) asserts that it is often misinterpreted as the probability that there is no effect, and advocates direct calculation of this probability by Bayesian methods. We disagree.

First, the prudent solution to misinterpretation of

classical *P* values is improved explication rather than dumping the methods.

Second, Bayesian conclusions depend on subjective prior probabilities, which are likely to vary widely, especially in adversarial situations; there is a risk that debates about effects will focus less on the data and more on the credentials of the "experts" whose priors are invoked. For example, Reckhow (1990) claims that *P* values are misleading because Bayesian calculations of the probability of no effect by Berger and Sellke (1987) are usually much larger. But these calculations are based on a prior probability of ≈ 0.5 that there is indeed no effect. In most assessment problems we would regard this prior probability as quite unrealistic: there is almost certainly *some* effect, so the prior probability of no effect should be close to 0; the Bayesian posterior probability of no effect could then easily be smaller than the *P* value.

Third, and most important: neither a *P* value nor a Bayesian posterior probability, for a null hypothesis that is inherently implausible, is adequate for such purposes as making decisions about ending or mitigating the impact, resolving legal disputes, designing future power plants or sewage outfalls, managing ecosystems, or studying the biological mechanisms involved (e.g., National Research Council 1990:76). The important questions are how large the effects are, and whether they matter. The main statistical tasks are estimating effect sizes and estimating the precision of these estimates, not hypothesis testing.

For this, there is a standard classical format, confidence intervals. There are Bayesian alternatives, but the disagreement between the two is usually minor for large or moderate sample sizes (Pratt 1965), provided that the prior distribution does not have a sharp peak. In assessments, where there are usually many interacting species, environmental parameters and physiological processes, many of them poorly understood, we would expect honest prior distributions to be quite diffuse.

Any test can be used to form a confidence interval for the size of the effect: the confidence interval is the set of values, δ , for which the null hypothesis "the change in the difference of the means is δ " is accepted. For many parametric tests, this interval is as easily calculated as the test itself. Randomization tests are much harder to convert, although efficient algorithms exist for some special cases (Pagano and Trichtler 1983, Trichtler 1984).

But not all parametric tests will lead to useful estimates in the assessment problem. If a transformation is needed for additivity, the test will concern the mean difference of transformed data; the ecological significance of a change in this mean may be obscure. In some cases there may be no suitable transformation, e.g., if the "Control" population density is greater than the Impact density in winter but smaller in summer, no monotone transformation can achieve additivity.

Perhaps most important, real perturbation effects might not be constant, even if we have the correct transformation. They may vary seasonally or in response to other conditions. For example, the cooling water system of the San Onofre Nuclear Generating Station may reduce irradiance (and gametophyte survival) over the San Onofre Kelp bed when the current flows South, but increase it when the current flows North (Murdoch et al. 1989).

One way to deal with these problems is to think of the "Control" density and other variables (e.g., season, current direction, water temperature, etc.) as predictors. Using regression methods on the Before data, we could estimate the function that best predicts the Impact area density from these predictors. The perturbation effect could be estimated as the difference between this function and the corresponding function obtained from the After data. This approach allows for effects that vary with environmental conditions, includes quantitative estimates of uncertainty (via confidence bands), and is conducive to graphical presentation, which many audiences may find easier to understand. At least one successful example of this approach already exists (Mathur et al. 1980).

This would not usually be a "clean" approach. It would involve regressions based on guessed functional forms, which would be checked, in part, by formal statistical tests, themselves often approximate. Few, if any, of the confidence intervals could be regarded as exact. Increasing exactness, e.g., by incorporating the uncertainty over functional form into the confidence interval, would be a difficult task, requiring some arbitrary judgments, and probably of little use to readers.

But restricting consideration to questions that allow formally exact answers (or appear to), such as overall tests for an effect, risks losing the information of most value: "Far better an approximate answer to the right question, which is often vague, than an exact answer to the wrong question, which can always be made precise" (Tukey 1962).

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BOCACCIO

History of the Fishery

Bocaccio (*Sebastes paucispinis*), sometimes called red snapper, rockcod, grouper, salmon grouper, or tomcod (as juveniles), was the dominant rockfish in California's early longline fishery. It was the most abundant rockfish in the otter trawl fishery from Morro Bay to Fort Bragg until the mid-1980's. By 1989 two-thirds of the bocaccio landed were taken by otter trawl, with the remainder being taken by set net, longline, and the recreational fishery.

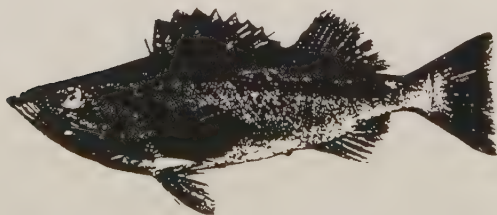
Accurate estimation of commercial bocaccio landings began in 1978. In the late 1970's, trawl landings averaged approximately four million pounds per year. Landings increased sharply, peaking in 1981 at about 10 million pounds, then gradually fell to about eight million pounds in 1984. Landings plummeted to near 2.5 million pounds by 1985 and have remained near this lower level. In 1978, nearly 40 percent of the sampled trawl landings contained half or more by weight bocaccio, but by 1990 less than 15 percent did. Since 1985, chilipepper has replaced bocaccio as the dominant rockfish in trawl landings.



California commercial landings of the bocaccio-chilepepper rockfish group, 1979-1991.

Recreational catches of bocaccio are generally made on rocky reefs by partyboat fishermen at depths of 250 to 750 feet. In some years, however, juveniles concentrate in shallow sandy areas near piers off central and southern California, where they are easily taken on small baited hooks. Estimated catches for the recreational fishery are available from 1980 onward and averaged 27 percent of the trawl landings over the same period. Recreational catches since 1984 have showed the same decline as the trawl fishery. In general, the recent recreational catches have been greater in southern California than in northern California.

Since 1982, bocaccio have been managed under the Groundfish Management Plan of the Pacific Fishery Management Council. In response to concerns about stock condition, the Council established for the first time, a harvest guideline of 2.4 million pounds for 1991.



Bocaccio rockfish, *Sebastes paucispinis*.

Status of Biological Knowledge

Bocaccio range from central Baja California to Kodiak Island, Alaska and are common from northern Baja California to the Washington-British Columbia border. Migration and movements of bocaccio are not understood.

Among rockfishes, bocaccio are noted for their relatively rapid growth, large adult size, and high variation in year-class strength. They are known to attain a length of 36 inches, a weight of 15 pounds, and a maximum age of about 50 years. Some fast growing individuals are caught with trawl gear at age one, and substantial numbers are landed by age two at lengths of about 16 inches.

Bocaccio are live-bearing fish. At extrusion (release), larvae are about 0.25 inch in length and absorb yolk from the egg stage during the first eight to 12 days. They grow rapidly to about seven inches by the end of their first year. A few mature when they are three years old, about 14 inches long and one pound. Fifty percent are mature at 16.5 inches and four years. Males mature at a slightly smaller size than females. By the time they are 10 years old, they average over 24 inches and weigh five pounds. The number of developing eggs increases from 20,000 in a 15-inch fish to about 2.3 million in a fish 30.5 inches long.

Off central and northern California, larval release occurs from January through May, peaking in February. In southern California spawning takes place from October through July, peaking in January. In central California, most larvae that survive to the juvenile stage are born in January and February, but months of successful reproduction can shift substantially from year to year. In southern California, some females produce as many as three broods in a season, but multiple brooding is uncommon farther north.

Larval bocaccio are initially pelagic and are most common within 100 feet of the sea surface, where they feed on plankton. Larval bocaccio have been captured in plankton nets as far as 300 miles from shore. By late May or early June, they settle to the bottom at lengths of 1.5 to 2.5 inches, often in kelp beds. Before completing their first year of life, these fast growing young of the year start eating the young of other rockfishes, surfperch, jack mackerel, and various small inshore fishes. Adults are found from depths of 60 to 1550 feet. They feed on smaller rockfishes, sablefish, anchovies, lanternfish, and squid.

Status of Population

During the past decade bocaccio landings have been dominated by the 1977 and 1984 year classes. As a consequence of the high variability in year-class strength, the size and age structure of the population fluctuates greatly over time. It appears that recruitment in the late 1960's and early to mid-1970's was, on average, substantially higher than average recruitment over the 1978-1989 period.

Stock analyses, using fishery age-composition data, recreational effort data, and trawl survey data, strongly indicate that biomass and spawning stock size have declined substantially over the 1978-1989 period. Estimated biomass has fallen from about 150 million pounds in 1978 to approximately 20 million in 1989. The recommended yield for all fisheries combined ranged from 1.6 million to 3.4 million pounds compared to 1989 landings of 2.6 million pounds.

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ECONOMIC UTILIZATION OF OCEAN RESOURCES

Background

Economic as well as biological factors affect the utilization of California's living marine resources. A particularly notable economic phenomenon has been the increase in trade activity between the domestic seafood industry and its foreign counterparts. California's commercial landings are increasingly being marketed abroad, and California consumers are satisfying their cosmopolitan taste for seafood with an array of imported products.

The economic value of a commercial fishery is appropriately measured by the benefits that it provides to consumers and the net economic return (gross revenue minus costs) that it generates to businesses at the ex-vessel, wholesale and retail levels. This chapter's discussion of commercial landings considers only the ex-vessel component of value, and reflects gross rather than net economic return in that it ignores the cost of harvesting fish. Similarly, the discussion of seafood imports and exports includes only the wholesale component of value and ignores costs incurred by import/export businesses. These ex-vessel and wholesale values provide a useful but incomplete picture of the economic value of California's commercial fisheries.

All monetary estimates of value provided in this chapter have been corrected for inflation and are expressed in 1990-equivalent dollars.

Supply

Trends in Landings and Revenues. Seasonal and annual variations in commercial landings are affected by a variety of factors, including species abundance and availability, management restrictions, market demand, ex-vessel prices, harvesting and processing technology and weather. The picture is further complicated by the multispecies nature of many fishing operations (For instance, small combination boats target salmon and albacore with troll gear and crab with pot gear, round haul vessels target pelagic wetfishes, squid, bonito and bluefin tuna; trawlers target rockfish, sablefish, Pacific whiting, flatfish and shrimp). In multispecies fisheries, fishing strategies, and therefore, landings of each species are affected by the availability and profitability of all species targeted in the fishery. Trends in landings are properly viewed in the context of these contributing factors and the interactions among them.

The State of California requires poundage landed, price received, and other information, to be recorded on a "pink ticket" each time a commercial fishing vessel lands its catch at a California port. The landings described in this chapter are based on pink ticket data and reflect most of the harvest but exclude discards, live bait catch and capture of live specimens for aquarium use. In particular:

1) Commercial fishing operations often yield a bycatch of non-targeted species, which may be landed and sold or discarded at sea. Even targeted species may be discarded if, for instance, they are sub-legal or non-marketable in size, or part of a catch that exceeds a trip limit. Information on the level of discards and discard mortality is generally unavailable.

2) Live bait sold in the recreational fishery is generally not landed, since transactions between buyers and sellers of live bait take place at sea or from receivers that are tied up near the docks. Logbook data indicate that bait haulers harvest up to twelve million pounds of live bait per year, most of which consists of northern anchovy.

3) A variety of marine specimens are harvested live, for display in home and public aquariums. These include animals such as gobies, juvenile sheepshead, juvenile leopard shark, and even "live rocks" (pieces of substrate with attached communities of living organisms). The harvest of such specimens, though not recorded on pink tickets, has likely increased in recent years, due to increases in domestic and foreign demand.

Total finfish and shellfish landings in California declined by almost half from 1970 to 1990, while total U.S. landings doubled over the same period. California's share of the U.S. harvest, which was 14 percent in 1970, declined to four percent by 1990. Ex-vessel revenues followed a similar pattern (Table 1).

Table 1. Commercial landings (1,000 lbs. landed weight) and ex-vessel revenues (\$1,000's) in 1990-equivalent dollars of finfish and shellfish in California and the United States in 1970, 1975, 1980, 1985 and 1990.

Year	Landings (1,000 pounds)	
	California	United States
1970	703,216	4,917,220
1975	861,315	4,877,443
1980	800,723	6,482,354
1985	356,960	6,257,642
1990	395,753	9,708,421
Year	Ex-Vessel Revenues (\$1,000's)	
	California	United States
1970	290,551	2,065,417
1975	307,900	2,372,577
1980	501,121	3,548,572
1985	154,002	2,825,643
1990	158,851	3,572,437

The major reason for California's diminished profile was the nine-fold decline in tuna landings from 1970 to 1990 (see appendix for landings figures). The proportion of ex-vessel revenues from all species attributable to tuna decreased from 74 percent in 1970 to 17 percent in 1990 (Table 2). High interest rates, the relocation of tuna processing operations from California to American Samoa and Puerto Rico, and competition from imports of canned tuna packed in water created economic hardship for the fishing fleet. Tuna landings in California dropped precipitously as many of the superseiners transferred flags or converted to other fisheries.

In 1970, California's top revenue-generating species were yellowfin (\$141.1 million), skipjack (\$40.7 million) and albacore (\$26.4 million); together, these three tunas accounted for 72 percent of total revenues from all species. By 1990, the top revenue-generating species had become sea urchin (\$24.7 million), yellowfin tuna (\$19.7 million), rockfishes (\$16.9 million), Dungeness crab (\$16.3 million) and chinook salmon (\$11.3 million), together accounting for 56 percent of total revenues from all species. California's commercial fishing industry, once dominated by the tuna fishery, has evolved into a more heterogeneous mix of smaller fisheries.



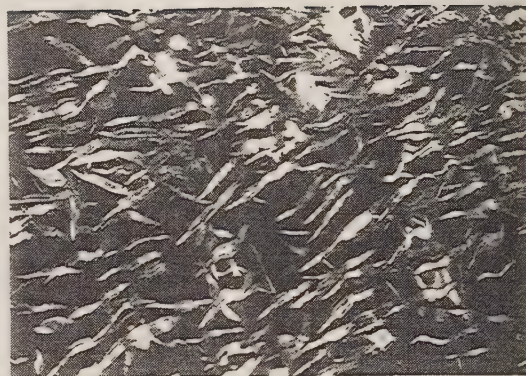
Commercial fishing vessel at San Pedro.

In addition to the tuna fishery, a number of other fisheries have also experienced a decline in recent years. For instance, both biological and economic factors (e.g., habitat loss, competition from aquaculture) have contributed to the decline in salmon landings. Concerns about abalone stocks have prompted increasingly restrictive management measures to reduce fishing effort, and abalone harvest has declined despite a strong market. Anchovy landings have fallen dramatically since 1983, when the decline in the ex-vessel reduction price prompted the round haul fleet to redirect their fishing effort to higher-priced species such as mackerel and squid.

Landings and ex-vessel revenues attributable to species other than tuna increased from \$74.7 million in 1970 to \$131.9 million in 1990, indicating that declining harvests of some species have been more than offset by increases in others. For instance, mackerel landings increased dramatically in the late 1970's, when the Pacific mackerel population rebounded to levels of abundance not experienced since the early 1940's. Market demand for calamari has prompted the upward trend in squid landings, which reached a record high of 62.7 million pounds in 1990.

A number of major fisheries in California are driven by market demand in the Pacific Rim. For instance, the fishery for red sea urchins developed in the early 1970's, when California gained access to the Japanese market for "uni" (sea urchin gonads, also referred to as roe for marketing purposes). Currently, about 50 percent of all urchin roe imported by Japan originates in the U.S. and over 75 percent of the U.S. product originates in California. In addition to being marketed fresh in Japan, California uni is also sold in the growing domestic sushi market.

Pacific herring landings also increased significantly during the 1970's, as California fishermen obtained access to Asian



Market squid (*Loligo opalescens*) gathered under lights at right.

markets. The harvest is shipped frozen to South Korea, where the roe is stripped and sold as a delicacy in Japan. Although prices have declined and stabilized from the record high of 1980, the fishery generates higher ex-vessel revenues than any other pelagic wetfish species.

The expansion of California's groundfish fishery during the 1970's was fueled by expanding markets as well as improvements in harvesting and processing technology. Asia is the major market for thornyheads, sablefish and other groundfish species.

Many of California's fledgling fisheries are also driven by Asian markets. The hagfish fishery developed in response to a hagfish shortage in the Republic of Korea, where the meat is eaten and the skin made into leather goods. Herring roe on kelp is packed in brine on kelp fronds and marketed as a delicacy in Japan. Landings of sea cucumber (boiled, dried and salted for sale in foreign and domestic Asian markets) doubled between 1985 and 1990. An experimental fishery has recently developed for purple sea urchins for both the roe and live sea urchin markets in Japan. Live fish markets that cater to California's own Asian population have developed for spot prawns, cabezon, California sheephead, white croaker and other small fishes.



Part of the commercial fishing fleet owned by immigrant families from Vietnam at Moss Landing harbor.

A fishery which has been virtually inactive during 1970-1990, but has perhaps the greatest potential for development, is

Pacific sardine. During the heyday of the sardine fishery (1934-1945), California landings averaged 1.1 billion pounds per year and accounted for almost 80 percent of total statewide landings of all species. The late 1940's signalled the beginning of what was to be a long term collapse of the fishery. Subsequent State restrictions on sardine harvest culminated in 1974 with a moratorium on all directed harvest and a small allowance for

incidental take. The State lifted its moratorium in 1986 and currently allows modest levels of directed and incidental harvest. Once sufficiently recovered, the sardine population may be able to sustain an annual yield of 500 million pounds. Whether and when this actually occurs will depend on the timetable for recovery of the stock and development of markets for sardine products, both of which are highly uncertain at this time.

Table 2. Ex-vessel revenues (in 1990-equivalent dollars) from finfish and shellfish in California in 1970, 1975, 1980, 1985 and 1990, by species category (\$1,000's).

Species	1970	1975	1980	1985	1990
CRUSTACEANS					
Dungeness Crab	13,432.5	6,781.6	15,496.8	10,844.0	16,273.8
Pac. Ocean Shrimp	1,910.6	1,615.5	3,464.8	1,442.2	4,184.1
Spiny Lobster	903.8	1,042.9	2,140.2	2,362.0	3,962.3
Rock Crab	201.1	642.6	1,219.1	1,867.2	1,813.9
Spot Prawn	55.2	488.8	718.8	401.0	1,526.0
Bay Shrimp	3.7	6.8	0.0	0.0	489.5
Ridgeback Prawn	0.0	38.9	321.8	669.0	152.5
Other	0.0	82.4	19.2	85.5	347.6
Total	16,506.9	10,699.5	23,380.7	17,670.9	28,749.7
TUNA					
Yellowfin	141,099.4	149,560.2	178,485.0	18,061.6	19,719.9
Bonito	2,194.3	9,463.6	4,511.5	712.3	1,934.8
Albacore	26,428.3	12,237.9	15,156.0	8,997.7	1,794.9
Bluefin	5,375.5	9,753.4	5,185.3	3,576.3	1,786.2
Skipjack	40,703.3	41,480.0	145,883.7	2,335.1	1,676.4
Other	11.5	291.8	2,055.2	1,102.1	83.7
Total	215,812.3	222,786.9	351,276.7	34,785.1	26,995.9
ECHINODERMS					
Sea Urchin	0.0	1,493.1	5,813.5	5,876.3	24,714.8
Other	0.0	0.0	8.6	18.3	35.9
Total	0.0	1,493.1	5,822.1	5,894.6	24,750.7
ROUND FISH					
Rockfish:					
Thornyhead	0.0	0.0	1,228.0	1,971.7	4,575.0
Sculpin	156.3	172.7	80.9	37.2	165.9
Other	2,777.4	7,808.5	12,302.9	12,991.4	12,199.9
Subtotal	2,933.7	7,981.2	13,611.8	15,000.3	16,940.8
Sablefish	1,075.6	3,401.1	2,781.8	3,432.1	3,487.2
Pacific Whiting	0.7	4.9	172.7	479.4	777.7
Total	4,010.0	11,387.2	16,566.3	18,911.8	21,205.7
PELAGIC WET FISH					
Pacific Herring	124.0	533.7	26,514.7	7,325.2	7,014.0
Mackerel	6,503.3	4,149.8	15,440.4	9,511.5	5,775.8
Northern Anchovy	7,266.7	12,166.3	4,039.5	338.8	604.1
Pacific Sardine	341.2	0.7	6.7	1.7	178.6
Total	14,235.2	16,850.5	46,001.3	17,177.2	13,572.5
SALMON					
Chinook	N/A	N/A	N/A	N/A	11,299.7
Coho	N/A	N/A	N/A	N/A	621.4
Other	N/A	N/A	N/A	N/A	125.2
Total	17,183.7	16,936.6	21,233.4	14,239.9	12,046.3
FLAT FISH					
Dover Sole	4,153.4	6,090.4	5,803.6	7,651.9	3,681.7
California Halibut	307.2	870.7	1,636.6	2,777.6	2,126.7
Petrale Sole	1,788.7	1,902.9	1,692.4	1,694.5	1,220.6
English Sole	1,090.4	1,936.7	2,125.0	970.9	682.6
Sanddab	236.8	459.2	665.4	449.2	437.0
Rex Sole	639.4	739.3	1,006.6	860.1	428.3
Sand Sole	78.2	94.0	217.5	217.8	156.7
Other	77.5	254.1	390.8	261.8	95.4
Total	8,371.6	12,347.3	13,537.9	14,883.8	8,829.0

Table 2. (continued)

Species	1970	1975	1980	1985	1990
MOLLUSKS					
Market Squid	2,245.8	2,007.9	4,812.9	4,517.9	4,683.7
Abalone:					
Red	N/A	1,415.6	1,622.8	1,545.0	1,845.9
Black	N/A	555.1	971.7	956.2	381.1
Green	N/A	331.4	223.0	124.9	178.9
Pink	N/A	908.6	461.3	314.1	140.0
Other	N/A	165.4	8.4	16.2	1.9
Subtotal	3,191.7	3,376.1	3,287.2	2,956.4	2,547.8
Other	3,528.6	2,700.7	1,962.7	176.1	58.0
Total	8,966.1	8,084.7	10,062.8	7,650.4	7,289.5
SWORDFISH	1,798.8	3,392.9	4,983.4	16,336.3	7,140.0
NEARSHORE FISHES					
Lingcod	467.2	1,025.2	1,046.9	555.2	931.2
Calif. Sheephcad	1.3	2.7	5.2	22.8	456.4
White Croaker	150.2	226.4	484.3	639.2	341.2
White Seabass	1,300.9	1,613.3	1,903.6	294.6	287.0
Other	400.2	357.4	587.8	431.0	300.9
Total	2,319.8	3,225.0	4,027.8	1,942.8	2,316.7
HAGFISH	0.0	0.0	0.0	0.0	2,118.2
SHARKS/RAYS/SKATES					
Mako Shark	N/A	N/A	157.8	234.7	741.8
Common Thresher Shark	N/A	N/A	1,960.2	2,200.5	641.3
Pacific Angel Shark	N/A	N/A	47.3	700.9	164.7
Soufin Shark	N/A	N/A	126.7	257.6	102.7
Other	N/A	N/A	1,307.6	298.4	155.6
Total	182.9	318.5	3,599.6	3,692.1	1,806.1
HERRING ROE ON KELP	0.0	0.0	0.0	0.0	1,525.4
SMELTS	269.1	201.6	226.2	310.0	235.0
SUBTOTAL	289,656.4	307,723.8	500,718.2	153,494.9	158,580.7
OTHER	894.1	175.8	403.2	506.6	270.6
GRAND TOTAL	290,550.5	307,899.6	501,121.4	154,001.5	158,851.3

Imports and Exports. The U.S. has experienced a persistent trade deficit with regard to seafood products. The value of U.S. imports of edible fishery products more than doubled from \$2.4 billion in 1970 to \$5.2 billion in 1990. Exports, although significantly lower in value than imports, increased almost tenfold from \$0.3 billion in 1970 to \$2.8 billion in 1990 (Table 3).

California's seafood trade deficit is disproportionately large. In 1990, the value of imported seafood products exceeded the value of exported products by two to one for the U.S. as a whole (Table 4) and by almost eight to one for California (Tables 5 and 6). About 28 percent (\$1.5 billion) of the imported value of fishery products in 1990 entered the U.S. at a California port. By comparison, California's share of U.S. exports in 1990 was a relatively modest seven percent (\$0.2 billion).

The past two decades have seen the development of a global market for fishery products and the increasing prominence of Pacific Rim countries as trading partners. Whereas 29 percent of the value of U.S. exports involved trade with Asia in 1970, this proportion had increased to 71 percent by 1990 (Table 3). Our major trading partners in 1990 were Japan (\$1,785.9 million) and Canada (\$313.6 million). The import picture is more diverse. In

1990, Asia and North America each accounted for about one-third of the value of U.S. imports (Table 3). More than half of U.S. imports in 1990 originated from the following five countries: Canada (\$1,174.5 million), Thailand (\$592.2 million), China (\$399.4 million), Ecuador (\$340.6 million) and Mexico (\$278.9 million).

The species composition of imports and exports differs somewhat between California and the U.S. as a whole. Shrimp accounted for 52 percent of the value of foreign imports into California (Table 4) and 31 percent of imports into the U.S. (Table 6) in 1990. Fresh and frozen salmon accounted for percent of the total value of U.S. exports (Table 6) but only four percent of the value of California's exports (Table 5). Fresh sea urchin was California's major exported product in 1990, accounting for 23 percent of the value of all seafood exported from the State (Table 5).

The seafood industry in California has created business opportunities for numerous processors, importers, brokers, traders and distributors. While the import/export figures (Tables 4 and 5) are indicative of the size of the seafood market in California, the complex and circuitous interactions among

middlemen make it difficult to trace imports and exports to their final destination. Imports are not necessarily consumed in the state of entry. For instance, some seafood imports that enter the U.S. at Nogales, Arizona and Honolulu, Hawaii likely end up in California markets. In addition, it is not safe to assume that exports from a state were necessarily produced within that state. For instance, much of the abalone exported from California is harvested in Mexico and funneled to other countries via California.

Despite the difficulty of determining exactly how much of the seafood imported into the U.S. ends up in California markets, available information suggests that Californians rely heavily on imports to satisfy their substantial demand for seafood. By one estimate, less than 10 percent of the seafood sold in California is derived from California fisheries; 13 percent comes from Pacific Northwest and Alaska fisheries, and most of the remainder consists of foreign imports.

Table 3. Value in 1990-equivalent dollars of U.S. imports/exports of edible fishery products by continent of origin/destination in 1970, 1975, 1980, 1985 and 1990 (\$1,000's).

IMPORTS FROM:	1970	1975	1980	1985	1990
Asia	587,756	696,697	993,671	1,374,528	1,954,106
North America	971,795	1,391,666	1,798,200	1,732,183	1,729,076
South America	220,344	312,849	474,884	707,176	764,016
Europe	304,309	614,229	612,851	762,636	487,013
Australia	183,455	160,851	258,673	274,233	262,376
Africa	106,531	145,092	116,266	86,141	36,578
TOTAL	2,374,190	3,321,384	4,254,545	4,936,897	5,233,165
EXPORTS TO:	1970	1975	1980	1985	1990
Asia	85,140	190,190	706,158	881,539	1,983,666
Europe	112,769	263,625	393,907	150,043	425,523
North America	86,077	185,623	273,014	166,517	343,980
Australia	4,409	7,196	37,318	25,392	20,493
Africa	1,283	1,482	10,551	1,794	3,611
South America	1,614	1,399	13,522	1,872	2,177
TOTAL	291,292	649,515	1,434,470	1,227,157	2,779,450

Table 4. Value of 20 top imports of edible fish and fish products into California from foreign countries in 1990 (\$1,000's).¹

Product Category	Value
Shrimp, frozen	774,940
Misc., frozen	129,912
Lobster, frozen	91,178
Tuna, canned	76,547
Tuna, prepared	64,387
Mollusk, frozen	45,299
Abalone, prepared	35,209
Misc., fresh	23,377
Mollusk, live	19,291
Shrimp, canned	18,263
Squid, frozen	15,770
Oyster, canned	14,828
Crab, canned	13,667
Sardine, prepared	13,003
Tuna, fresh	11,941
Misc., prepared	10,799
Salmon, fresh	10,524
Crab, frozen	8,880
Clams, canned	7,724
Crustacean, frozen	7,715
Other	97,746
TOTAL	1,491,000

¹Source: Unpublished data from U.S. Bureau of the Census.

Table 5. Value of 20 top exports of edible fish and fish products from California to foreign countries in 1990 (\$1,000's).¹

Product Category	Value
Sea urchin, fresh	44,436
Abalone, prepared	30,392
Misc., frozen	15,750
Cod, frozen	11,235
Roe, frozen	9,695
Lobster, frozen	9,383
Shrimp, frozen	7,344
Misc., dried	7,257
Squid, frozen	6,793
Herring, frozen	6,726
Salmon, frozen	5,928
Squid, prepared	4,772
Tuna, fresh	3,012
Clams, frozen	2,263
Mollusk, prepared	2,175
Salmon, canned	1,900
Crab, frozen	1,868
Salmon, fresh	1,855
Shrimp, canned	1,491
Sablefish, frozen	1,470
Other	17,255
TOTAL	193,000

¹Source: Unpublished data from U.S. Bureau of the Census.

Table 6. Value of U.S. exports, imports and net exports of fishery products in 1990, by product category (\$1,000's).

Product Category	Exports	Imports	Net Exports
FRESH & FROZEN:			
Shrimp	112,212	1,639,181	-1,526,969
Fillets	66,320	809,932	-743,612
Lobster	82,622	439,972	-357,350
Tuna	45,085	339,300	-294,215
Blocks	214,679	373,292	-158,613
Scallop	19,518	130,453	-110,935
Groundfish ¹	298,568	79,987	218,581
Salmon	666,583	252,880	413,703
Other Fish and Shellfish	814,885	456,311	358,574
Total	2,320,472	4,521,308	-2,200,836
CANNED:			
Salmon	104,277	4,241	100,036
Tuna	13,211	293,873	-280,662
Other	68,140	244,510	-176,370
Total	185,628	542,624	-356,996
CAVIAR & ROE	223,836	15,007	208,829
CURED	32,831	118,581	-85,750
OTHER	16,683	35,645	-18,962
GRAND TOTAL	2,779,450	5,233,165	-2,453,715

¹"Groundfish" includes all fresh and frozen product forms (except fillets and blocks) of cod, haddock, hake, pollock, sablefish and flatfish. "Fillets" and "Blocks" cover a variety of species, including groundfish.

Demand

During 1986-1988, U.S. consumption of fish and shellfish averaged 45.2 pounds per capita (live weight equivalent). Similar consumption rates can be found in Western Europe and Canada. Consumption rates in northern Europe and industrialized Asian countries are two to four times the U.S. average, while consumption rates in Mexico and other less industrialized countries tend to fall below the U.S. average (Table 7).

Consumption of commercial finfish and shellfish in the U.S. (edible meat) increased from about 24.0 billion pounds in 1970 to 38.8 billion pounds in 1990. The reasons for this are twofold: a 23 percent increase in the U.S. population and a 31 percent increase in per capita consumption, from 11.8 pounds in 1970 to 15.5 pounds in 1990. About two-thirds of total consumption is accounted for by fresh and frozen products (Table 8).

Assuming that per capita seafood consumption in California is equal to the national averages described in Table 8, total consumption in California (edible meat) is estimated to have increased from approximately 2.4 billion pounds in 1970 to 4.5 billion pounds in 1990. These, however, should be considered conservative estimates, since the strong seafood preferences exhibited by sizeable segments of California's population (e.g., upscale health-conscious consumers, Asian immigrants) suggest that per capita consumption in California likely exceeds the national average.

Table 7. Annual per capita consumption of fish and shellfish in selected countries, 1986-88 average (pounds live weight equivalent).

Country	Pounds Live Weight
Iceland	203.7
Japan	157.0
Portugal	132.5
Hong Kong	112.2
Republic of Korea	109.3
Norway	97.7
Spain	83.8
France	63.9
Canada	59.3
Peru	51.4
United States	45.2
United Kingdom	42.3
German Democratic Republic	33.5
Mexico	21.6
People's Republic of China	17.6
Brazil	14.6

Table 8. U.S. annual per capita consumption of commercial fish and shellfish by product category in 1970, 1975, 1980, 1985 and 1990 (pounds edible meat).

Product Category	1970	1975	1980	1985	1990
Fresh and Frozen	6.9	7.5	7.9	9.8	10.1
Canned	4.5	4.3	4.3	5.0	5.1
Cured	0.4	0.4	0.3	0.3	0.3
TOTAL	11.8	12.2	12.5	15.1	15.5

Outlook

California's commercial fishing industry, once dominated by the tuna fishery, has evolved into a more heterogeneous mix of smaller fisheries. Many of these fisheries have developed in response to demand in Pacific Rim countries (most notably Japan). Future fishery development in the State will depend largely on the ability of the industry to compete in the global seafood market. This ability will depend, not only on the quantity and quality of domestically caught seafood, but also on success in overcoming barriers to trade.



The dory fleet at Newport Beach where fishermen have marketed their catch directly to consumers for many decades.

Commercially caught seafood must also compete with aquaculture products for the consumer's dollar. Aquaculture contributes significantly to the worldwide trade in seafood products. While the competition offered by farm-raised imports (particularly salmon and shrimp) probably reduces the ex-vessel prices received by U.S. fishermen, it also provides benefits to U.S. consumers in the form of lower seafood prices.

In addition to market pressures, California's commercial fisheries face growing competition from other users, including sport anglers and marine mammals (most notably sea otters and sea lions), for limited marine resources. Activities that alter the marine environment (such as oil and gas development, discharge of sewage, thermal and chemical wastes, diversion of water from instream to agricultural and

other uses, dredging of harbors, elimination of wetlands, and other forms of coastal development) also affect the abundance of marine resources.

Seafood safety is also an important health and economic issue. Quality control from harvest to market, and adequate inspection, provide important safeguards. However, even isolated instances of tainted seafood can erode consumer confidence, with significant repercussions for the entire industry.

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Mycardial sarcolemma isolated from skipjack tuna, *Katsuwonus pelamis*

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The high cardiac outputs observed in tuna compared with other teleosts may imply differences in the regulation of myocardial contractility. Sarcolemma is a critical organelle in the teleost heart in the regulation of intracellular calcium concentration and hence contractility. A procedure is described for the isolation of large quantities of highly purified sarcolemma from the skipjack tuna heart by differential and sucrose-gradient centrifugation in the presence of multiple protease inhibitors. The preparation was characterized using the sarcolemma marker K^+ -stimulated p -nitrophenylphosphatase ($K^+pNPPase$). From a starting ventricular wet weight of about 60 g, a yield of >20 mg sarcolemmal protein and a >43-fold purification over the crude homogenate were achieved. The percentage recovery of the total $K^+pNPPase$ in the sarcolemma fraction was greater than 14%. Both the purification index and recovery were substantially greater than those achieved with a much smaller scale sarcolemma preparation recently described for the trout heart. The equilibrium binding of the dihydropyridine PN200-110 and ryanodine were determined in these preparations. In purified sarcolemma, the dihydropyridine receptor binding density (B_{max}) and dissociation constant (K_d) were found to be 0.48 ± 0.07 pmol $\cdot$ mg protein $^{-1}$ and 0.09 nM respectively, similar to that found in mammals. In crude homogenates, the ryanodine receptor B_{max} was approximately 0.12 ± 0.04 pmol $\cdot$ mg protein $^{-1}$ and thus was a little more than half the value observed for the dihydropyridine receptor. The large-scale sarcolemma isolation procedure described in this paper for tuna may be useful for developing a better understanding of the role of the sarcolemma in the regulation of ventricular function in teleosts.

TIBBITS, G. F., KASHIHARA, H., et BRILL, R. W. 1992. Myocardial sarcolemma isolated from skipjack tuna, *Katsuwonus pelamis*. Can. J. Zool. 70: 1240–1245.

Les rendements cardiaques plus élevés chez les thons que chez d'autres téléostéens peuvent être attribuables à des différences dans le contrôle de la contractilité du myocarde. Le sarcolemme est un organe qui joue un rôle critique dans le cœur des téléostéens, puisqu'il contrôle la concentration de calcium intracellulaire et donc la contractilité. Nous décrivons ici une technique qui nous a permis d'extraire de grandes quantités de sarcolemme très purifié de cœurs de Thons à ventre rayé par centrifugation différentielle sur un gradient de sucrose en présence de multiples inhibiteurs de la protéase. La préparation a été caractérisée par l'utilisation d'un marqueur du sarcolemme la p -nitrophénylphosphatase stimulée par K^+ (la $K^+pNPPase$). À partir d'une masse ventriculaire fraîche d'environ 60 g, nous avons pu obtenir >20 mg de protéine de sarcolemme 43 fois plus pure que dans l'homogénat brut. Dans la fraction de sarcolemme obtenue, le pourcentage de marqueur récupéré était supérieur à 14%. L'indice de purification et la fraction récupérée étaient considérablement plus élevés que ceux qui peuvent être obtenus par une technique récemment décrite de préparation de sarcolemme de truite à échelle beaucoup plus petite. Les liaisons à l'équilibre de la dihydropyridine PN200-110 et de la ryanodine ont été déterminées pour ces préparations. Dans le sarcolemme purifié, le B_{max} du récepteur de la dihydropyridine et le K_d ont été évalués à $0,48 \pm 0,07$ pmol $\cdot$ mg protéine $^{-1}$ et 0,09 nM, valeurs semblables à celles qui prévalent chez les mammifères. Dans des homogénats bruts, le B_{max} du récepteur de la ryanodine était d'environ $0,12 \pm 0,04$ pmol $\cdot$ mg protéine $^{-1}$ et équivalait donc à un peu plus de la moitié de la valeur observée dans le cas du récepteur de la dihydropyridine. La technique d'extraction de sarcolemme sur une grande échelle, décrite ici dans le cas des thons, permettra sans doute d'obtenir une meilleure compréhension du rôle du sarcolemme dans le contrôle du fonctionnement ventriculaire chez les téléostéens.

[Traduit par la rédaction]

Introduction

Cardiac output, normalized per unit body mass, is substantially higher in the tuna relative to other teleosts and is comparable to that observed in mammals (Brill and Bushnell 1991). This is a consequence of both a higher operating heart rate (HR) and higher normalized stroke volume (SV) compared with other lower vertebrates. The observation that SV is substantially higher than that of other teleosts when expressed per unit body mass may be related to the following: (i) a ventricular mass that is several times higher than that of other teleosts when normalized per unit body mass, (ii) high venous return, and (iii) enhanced contractility. Clearly, the higher heart (or more importantly, left ventricle) to body weight ratio

is well documented (Farrell 1991) and is an important factor in the determination of SV. However, the tuna heart may also exhibit important differences in myocyte contractile function that are consistent with both the higher HR and SV. These would include the rates of Ca^{2+} delivery to and removal from the contractile element that determine the strength of cardiac contraction and the minimum duration of the cardiac cycle. Virtually nothing is known about these functions in the tuna heart.

It is well documented that myocardial sarcolemma (SL) is an important regulator of the intracellular calcium concentration ($[Ca^{2+}]_i$), which is crucial in the regulation of contractility (Langer 1980). At least three SL proteins are involved in the

regulation of $[Ca^{2+}]_i$ in the mammalian heart: Ca^{2+} ATPase, Na^+-Ca^{2+} exchange, and voltage-dependent Ca^{2+} channels (Carafoli 1987). Both Na^+-Ca^{2+} exchange and L-type voltage-dependent Ca^{2+} channels (LCC) were recently demonstrated in the trout heart (Tibbitts *et al.* 1990). LCC are known to bind dihydropyridines (DHP) with high affinity (Mikami *et al.* 1989) and thus can be quantified by DHP ligand binding. Furthermore, in the mammalian heart, the DHP receptor of the SL comes in proximity to and is implicated in the opening of the Ca^{2+} release channel of the sarcoplasmic reticulum (SR). Thus, in the mammalian heart, the opening of the LCC and the subsequent Ca^{2+} influx are prerequisites for the release of SR Ca^{2+} , the major source of contractile Ca^{2+} (Fabiato 1983). In lower vertebrates, however, the importance of SR Ca^{2+} release in contractility is not well established (Klitzner and Morad 1983; Tibbitts *et al.* 1991). Electron micrographs indicate that T-tubules are absent and that the SR is both sparse and poorly organized relative to that of higher vertebrates (Santer 1985). Furthermore, tension generation in cardiac tissue from lower vertebrates is insensitive to ryanodine in concentrations known to block the release of SR Ca^{2+} (Bers 1985; Driedzic and Gesser 1988).

The tuna heart, with a high HR and SV, may have a necessarily more complex system of Ca^{2+} regulation than other teleosts in order to meet these stringent demands. Thus this investigation was undertaken to obtain a better understanding of the molecular basis of Ca^{2+} regulation in the high-performance tuna heart. This article describes a suitable means of isolating large quantities of highly purified sarcolemma and some preliminary determinations of its properties.

Methods

Animal care and handling

Skipjack tuna, *Katsuwonus pelamis*, weighing 1–2 kg, were obtained from a local commercial fishing vessel and maintained in outdoor tanks at 24–26°C typically for 2–3 days at the Kewalo Research Facility in Honolulu.

Sarcolemmal isolation and characterization

Myocardial sarcolemma was isolated using modifications of techniques described for teleosts by Tibbitts *et al.* (1990) and for mammals by Philipson and Ward (1987). The principal solution used in the isolation procedure was homogenizing medium (HM), which contained, in mM: sucrose, 350; *N*-tris(hydroxymethyl)-2,2-aminoethanesulfonic acid (TES), 20 (pH 7.6 at 25°C); and dithiothreitol (DDT), 1. A second solution (HMI) was produced by adding the following protease inhibitors (with final concentrations indicated in μ M) to the HM: phenylmethylsulfonylfluoride (PMSF), 100; pepstatin A, 1; iodoacetamide, 1; benzamide, 0.75; and the following (in mg/mL): trypsin soybean inhibitor, 0.1; leupeptin, 0.05; phenanthroline, 0.1; and aprotinin, 0.05.

After the tuna was killed by a sharp blow to the head and an incision made ventrally, the heart (approximately 5 g) was excised quickly and then rinsed in HMI maintained at 4°C. The heart was trimmed of connective tissue, atria, and fat and then weighed. Twelve tuna ventricles were pooled to give a mean starting wet weight of about 60 g for each of the three separate isolations. The pooled ventricles were minced in about three volumes of HMI with scissors to about 2 mm³ and homogenized twice for 10 s each time in about four volumes of HMI in a chilled Waring blender set at high speed. The homogenate was brought to a volume of 290 mL with HMI, and 2 mL was removed for subsequent biochemical analyses of the crude homogenate (CH). The contractile proteins were solubilized by adding 32 mL of a KCl and Na₂PO₄ solution to the 288 mL of CH, bringing the final concentrations of KCl and Na₂PO₄ to 100 and 25 mM, respectively. The CH was spun at 20 000 $\times$ g for 35 min

at 4°C. After the supernatants were discarded, the pellets were homogenized in HM with a Polytron homogenizer at setting 5– until the pellets were resuspended. This suspension was spun at 20 000 $\times$ g for 35 min, and once again the supernatant was discarded and the pellet resuspended in HM with a Polytron homogenizer at setting of 5–6. The resultant suspension was spun at 38 000 $\times$ g for 45 min at 4°C.

These pellets were resuspended in six 5-mL aliquots of 45% sucrose. Six discontinuous sucrose gradients comprising 32, 30, 20, and 8% sucrose steps were layered on top. The gradients were spun in a swing bucket rotor (SW 28) at 122 000 $\times$ g for 16 h and each was fractionated into four tubes labeled F1 to F4 in order of increasing density. All fractions were diluted with roughly equal volumes of an ice-cold solution of 560 mM NaCl and 40 mM TES in order to avoid osmotic shock. The tubes were allowed to equilibrate for approximately 90 min on ice, after which they were slowly diluted with an ice-cold loading medium (LM) that contained 140 mM NaCl and 10 mM TES (pH 7.6 at 25°C). The suspensions were centrifuged at 180 000 $\times$ g for 1 h, and the pellets from F2 and F3 were resuspended in 3 mL LM (to give a final protein concentration of $\sim$ 6 mg $\cdot$ mL⁻¹), characterized as described below, and then frozen in liquid N₂. Protein determinations on all fractions were done by the method of Bradford (1976) using bovine serum albumin (BSA) as a standard. The SL marker K⁺-stimulated *p*-nitrophenylphosphatase (K⁺pNPPase) was assayed, as described by Tibbitts *et al.* (1981), in the crude homogenate and all fractions derived from the sucrose gradient. Purification index (PI) was defined as the ratio of the specific activity of K⁺pNPPase in the sarcolemmal fraction to that in the crude homogenate. Recovery was defined as the percentage of the total K⁺pNPPase activity (μ mol $\cdot$ h⁻¹) in the SL fraction compared with the crude homogenate.

Dihydropyridine binding

The binding of the dihydropyridine [³H](+)-PN200-110 was measured in both the crude homogenate and the F2 (SL-enriched) fraction derived from the sucrose gradients. The tubes contained (in a final volume of 5 mL) 20 mM TES (pH 7.6 at 25°C), 0.05–0.8 mM [³H](+)-PN200-110, and 2.5 mM CaCl₂. The amount of protein in each tube was approximately 25 μ g for F2 and 250 μ g for CH, and the binding reaction was allowed to proceed for 90 min in the dark at room temperature. Assays were performed in both the presence and the absence of 1 μ M unlabeled nifedipine to determine specific binding. All binding assays were conducted in dim (10 W) red light to prevent photoinactivation of the dihydropyridines. Binding was terminated by rapid vacuum filtration through GF/C (Whatman) filters. The filters were washed with three 4.5-mL aliquots of ice-cold buffer, placed in a vial, dried, and counted by standard liquid scintillation procedures.

Ryanodine binding

The binding of [³H]ryanodine to crude homogenates was carried out with minor modifications of the procedure described by Chu *et al.* (1988). The binding reaction was carried out with 160 μ g homogenate protein (at 28°C for 1 h) in a tube with a 1-mL final volume that contained the following: 11 nM [³H]ryanodine, nonradioactive ryanodine (Calbiochem) in concentrations of 0–500 nM, 150 mM KCl, 20 mM TES (pH 7.6 at 25°C), and 25 μ M CaCl₂. In pilot studies we determined that these conditions resulted in equilibrium binding. No buffers were added in an attempt to regulate free Ca^{2+} . The ryanodine was dissolved in ETOH and the final [ETOH] was less than 0.5%, which we determined previously to have no effect on the binding. After 1 h, the binding reaction was stopped by filtration through 0.45- μ m cellulose acetate filters. The filters were rinsed first with 2 mL of a solution containing 150 mM KCl and 10 mM TES (pH 7.6 at 25°C), and finally with 1 mL of a 10% ETOH solution. The dried filters were counted by conventional liquid scintillation procedures.

Materials

[³H](+)-PN200-110 and [³H]ryanodine were purchased from New England Nuclear and were used without further purification. With t

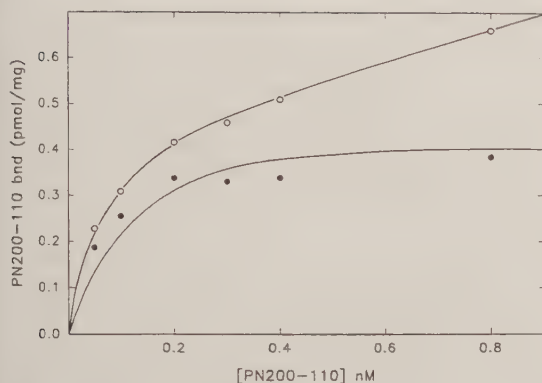


FIG. 1. Amount of [^3H]PN200-110 bound (bnd) to purified sarcolemma as a function of free [^3H]PN200-110 concentration. Both the total ($\circ$) and the specific ($\bullet$) binding are indicated.

TABLE 1. Protein yield (normalized per unit of ventricular wet weight) and specific $\text{K}^+\text{pNPPase}$ activity at 37°C (normalized per unit of protein) in the crude homogenate and various fractions from the sucrose gradient

	Protein yield	Specific $\text{K}^+\text{pNPPase}$ activity
Homogenate	103.59 ± 4.97	0.20 ± 0.02
F2	0.31 ± 0.03	8.66 ± 0.96
F3	0.17 ± 0.02	3.49 ± 0.56
F4	10.45 ± 2.56	0.21 ± 0.06

NOTE: Values are given as means $\pm$ SE. Protein yield is measured as $\text{mg protein} \cdot \text{g wet wt.}^{-1}$; specific $\text{K}^+\text{pNPPase}$ activity is measured as $\mu\text{mol} \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$.

TABLE 2. Recovery and purification index based on the activities of $\text{K}^+\text{pNPPase}$ in the crude homogenate and various fractions from the sucrose gradient

	Recovery (%)	Purification index
F2	14.7	43.3
F3	3.3	17.5
F4	8.8	1.1

exception of cold ryanodine, all other biochemicals were of the highest purity available from the Sigma Chemical Company.

Results

The large-scale SL isolation procedure developed for the tuna heart resulted in the isolation of large quantities of highly purified SL with a yield of $0.31 \text{ mg SL protein} \cdot \text{wet wt.}^{-1}$ (Table 1). The activities of the SL marker $\text{K}^+\text{pNPPase}$ in the crude homogenate and SL fraction were 0.20 and $8.66 \mu\text{mol} \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$ (Table 1). From these data, the calculated recovery of SL in F2 from the total SL pool was 14.7% and the purification index was 43.3-fold (Table 2).

Figure 1 illustrates the binding of the DHP [^3H](+)-PN200-

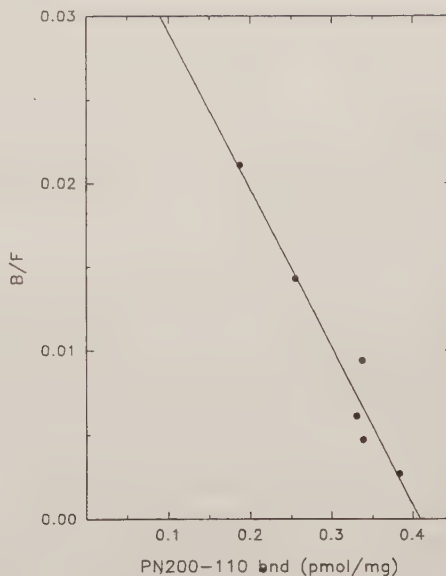


FIG. 2. Scatchard plot of the specific binding data shown in Fig. 1. A least-squares linear regression line is drawn through the data with a correlation coefficient of >0.95 . B/F, bound/free; bnd, bound.

110 to highly purified SL as a function of the free concentration of [^3H](+)-PN200-110 in a typical experiment. The specific binding between 0.05 and 0.20 nM [^3H](+)-PN200-110 was greater than 81% of the total binding. Total [^3H](+)-PN200-110 binding involved no more than 3% of the total ligand concentration. The specific binding data shown in Fig. 1 are presented as a Scatchard plot in Fig. 2. The correlation coefficient exceeded 0.95. Using three different SL preparations, the derived binding density (B_{max}) and dissociation constant (K_d) values for [^3H](+)-PN200-110 equilibrium binding to SL were $0.48 \pm 0.07 \text{ pmol} \cdot \text{mg protein}^{-1}$ and $0.09 \pm 0.01 \text{ nM}$, respectively. The binding of [^3H](+)-PN200-110 to crude homogenates from tuna ventricles was carried out in an identical manner, except more protein was included per tube. From a Scatchard plot (not shown) of these data, it was calculated that the B_{max} and K_d values in the crude homogenate were $0.24 \pm 0.04 \text{ pmol} \cdot \text{mg}^{-1}$ and $0.15 \pm 0.02 \text{ nM}$, respectively.

The [^3H]ryanodine binding was performed only with crude homogenate protein. The binding to crude homogenates proved to be difficult and not all experiments were successful, as judged by the consistency of the duplicates. The data presented represent those experiments in which the duplicates and goodness of fit were satisfactory. In Fig. 3, the specific binding of [^3H]ryanodine to crude homogenates is shown as a function of free ryanodine concentration from 22 to 511 nM . The specific binding at 22 nM represents more than 60% of the total binding of [^3H]ryanodine to this preparation. The Scatchard representation of these data is shown in Fig. 4, which has a correlation coefficient of >0.99 . In three different preparations, the derived B_{max} of ryanodine binding to crude homogenates was $0.12 \pm 0.04 \text{ pmol} \cdot \text{mg protein}^{-1}$.

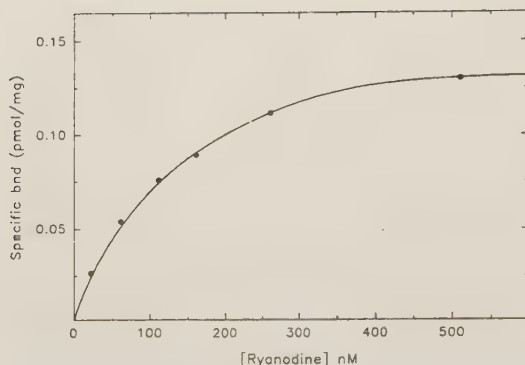


FIG. 3. Amount of ryanodine specifically bound (bnd) to crude homogenates as a function of the free ryanodine concentration.

Discussion

The protein yield of the crude homogenate found in the tuna ventricle ($103.6 \text{ mg} \cdot \text{g wet wt.}^{-1}$) is similar to that found in trout (Tibbitts *et al.* 1990) and mammalian (Tibbitts *et al.* 1989) ventricles. The specific activity of $\text{K}^+\text{pNPPase}$ in the crude homogenate, $0.20 \mu\text{mol} \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$, is only 31% of that observed in cold-adapted trout hearts (Tibbitts *et al.* 1990). Both of these assays were conducted at 37°C for comparison with mammalian values; however, the temperature dependence of this enzyme was evaluated in both teleost species, to determine whether $\text{K}^+\text{pNPPase}$ is denatured at 37°C and to determine the Q_{10} of the enzyme. There were no indications from the specific activities of $\text{K}^+\text{pNPPase}$ from teleost species that the enzyme denatures at 37°C . The calculated Q_{10} values were 2.8 ($21-37^\circ\text{C}$) and 2.4 ($7-37^\circ\text{C}$) in tuna and trout ventricles, respectively, which are similar to that observed in mammals (G. F. Tibbitts, unpublished observations). We have evidence that the high $\text{K}^+\text{pNPPase}$ activity in the cold-adapted trout heart is a component of the adaptation to cold (McKnight *et al.* 1989). The specific activity of $\text{K}^+\text{pNPPase}$ that we have observed in warm-adapted trout ventricles is about one-half that in cold-adapted heart (G. F. Tibbitts and H. Kashiwara, unpublished observations) and thus much closer to that observed in the tuna heart in the present study. These data probably reflect differences in densities of the enzyme in SL, but further experimentation is required to confirm this statement. Since the $\text{K}^+\text{pNPPase}$ activity reflects a component of the $\text{Na}^+ - \text{K}^+$ pump (Schwartz *et al.* 1975), this finding is consistent with the notion that the densities of ion pumps, which generally exhibit high Q_{10} values, must increase under colder conditions to maintain ionic gradients (Hochachka 1988). The tuna heart, functioning at $\sim 25^\circ\text{C}$, therefore may not require the high pump densities that are apparent in the cold-adapted trout.

The SL isolation procedure described in this paper was successful in producing a reasonable yield of highly purified membranes from the tuna heart. The fraction enriched in SL (F2), had a yield of $0.31 \text{ mg protein} \cdot \text{g wet wt.}^{-1}$, which is about two-thirds that achieved with a much smaller scale procedure using trout ventricles. However, the advantages of obtaining $\sim 20 \text{ mg}$ SL per isolation with this procedure versus $\sim 3 \text{ mg}$ with the small-scale approach are obvious. Further-

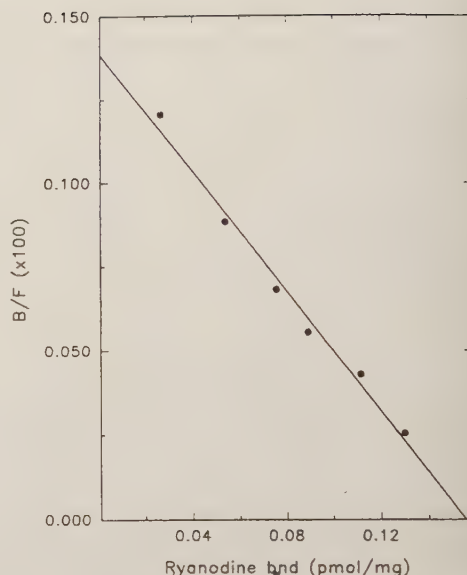


FIG. 4. Scatchard plot of the data shown in Fig. 3. A least-squares linear regression line is drawn through the data with a correlation coefficient of >0.99 . B/F, bound/free; bnd, bound.

more, the recovery and purification of SL from the tuna ventricles are about 2 and 3 times greater, respectively, than those obtained with trout by means of the procedure described previously (Tibbitts *et al.* 1990). The high specific activity of $\text{K}^+\text{pNPPase}$ of the SL preparation indicates a high degree of purity. However, the extent of cross contamination from other organelles cannot be precisely stated without determinations of markers of SR and other organelles, which could not be performed because of prevailing conditions.

DHP binding was examined in both crude homogenates as well as in purified SL fractions from the tuna ventricles, using $[^3\text{H}]\text{PN200-110}$. The K_d values derived from Scatchard analyses of these binding curves were similar to those reported in trout (Tibbitts *et al.* 1990) and mammalian hearts (Lee *et al.* 1984), suggesting a similarity in receptor structure across these phyla. The mean B_{max} values from homogenates and SL fractions were 0.24 and $0.48 \text{ pmol} \cdot \text{mg protein}^{-1}$, respectively. The homogenate B_{max} is about 40% lower than that observed in the cold-adapted trout heart. Again, there is reason to believe that the very high DHP B_{max} observed in the cold-adapted trout heart homogenate is, at least in part, a consequence of the cold adaptation (G. F. Tibbitts and H. Kashiwara, unpublished observations). The B_{max} values in the warm-adapted (15°C) trout are similar to those observed in tuna in the present study. The DHP B_{max} observed in the SL-enriched fractions from tuna in the present study ($0.48 \text{ pmol} \cdot \text{mg protein}^{-1}$) is approximately 15% of that found in purified SL in the cold-adapted trout heart. There are probably two explanations for this disparity. The first is based on the differences in the homogenates. From these data, we would therefore expect the tuna SL DHP B_{max} to be about 40% that of trout. We propose that this is a species difference, an explanation of which is offered below. The second reason may be related to the

higher SL purification realized in the present study and the observation that the DHP receptor does not copurify strictly with conventional SL markers. This is supported by what we and others have observed in mammalian species. Thus, the high purification observed in this study may be at the expense of recovered DHP receptor and components of the junctional complex. However, despite the fact that the DHP $B_{\max}$ in SL in the tuna heart is lower than that of trout, it should be noted that it is comparable to that observed in mammals (Glossmann *et al.* 1984).

The SR Ca^{2+} release channel, or ryanodine receptor, controls the efflux of Ca^{2+} from the SR to the cytosol (Meissner 1986), which in the mammalian heart is the largest source of Ca^{2+} delivered to the myofilaments (Wier 1990). Ryanodine inhibits force production in the mammalian heart (Sutko and Kenyon 1983) by binding with very high affinity to the release channel and affecting the opening of the channel in a dose-dependent manner (Meissner 1986). The binding of [^3H]ryanodine to crude homogenates allowed us to determine the relative density of the ryanodine receptor in this tissue. The $B_{\max}$ observed in this study, $0.12 \text{ pmol} \cdot \text{mg protein}^{-1}$, is similar to that observed by others (e.g., Pessah *et al.* 1985) in mammalian hearts.

Because of the difficulty with the ryanodine binding and a variety of other complications, we would prefer, at this stage, not to speculate about the stoichiometry of these receptors. We are not aware of ryanodine binding having been reported in cardiac tissue from other teleosts. These data suggest that there is a reasonable amount of SR Ca^{2+} -release channel protein in the tuna ventricle despite the apparent sparsity of SR observed in electron micrographs (Breisch *et al.* 1983). The function of the SR as a contributing source of Ca^{2+} is indicated further by the inhibition of atrial contractions by ryanodine in the study by Keen *et al.* (1992). As suggested previously (Tibbits *et al.* 1991), a reasonable hypothesis may be that the magnitude of SR releasable Ca^{2+} in the teleost heart is temperature dependent. It may be postulated that at lower ($<20^\circ\text{C}$) temperatures the channel remains open and the SR is unable to sequester Ca^{2+} , thus eliminating the SR as a functional Ca^{2+} -release site. Preliminary evidence to support this hypothesis comes from studies (L. Hove-Madsen, unpublished observations) using ventricular strips from the trout heart studied at different temperatures.

We propose, therefore, that the tuna heart may have a higher reliance on SR Ca^{2+} for contraction than other lower vertebrates. This may be the consequence of a more fully developed SR or simply the fact that the tuna physiological temperature range ($\sim 25^\circ\text{C}$) allows the SR Ca^{2+} -release channel to function appropriately. This hypothesis offers an explanation for the lower DHP $B_{\max}$ observed in this study; namely, there is less dependence on SL Ca^{2+} influx for contraction in the tuna heart. However, considering the observation that the L-type Ca^{2+} channel has a high Q_{10} (~ 3) in mammals (Cavalié *et al.* 1985), it is also possible that elevated operational temperatures in tuna do not necessitate high channel densities for adequate Ca^{2+} current. The notion of greater reliance on SR Ca^{2+} release for contraction offers some advantages to the tuna heart, most notably, higher rates of delivery and removal of Ca^{2+} from the contractile element. The latter would be consistent with the shorter cardiac cycle required for the high heart rates observed in these species (Brill and Bushnell 1991). It should be stated that because of the limited data from this species, these inferences must be

considered as no more than working hypotheses at this time. Much more extensive investigation (involving both biochemical and physiological approaches) is required before these hypotheses can gain acceptance.

In summary, we have been able to isolate highly purified SL in large quantities from the tuna ventricle. This procedure should permit experiments in the future that will offer a much greater understanding of the role of SL in myocardial function in teleosts than has heretofore been possible.

Acknowledgements

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3

*The rise and fall of the
California sardine empire*

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The plane circled slowly, searching. The US Navy pilot and crew had been trained to locate and report the position of the prey under the waves. Once sighted, a message would be sent to the US Navy Air Station ashore which then relayed the sighting to a subchaser or US Coast Guard cutter in the area. The warship would signal 10 to 15 pursuit vessels, inform them of the prey's reported location and the hunt would begin (Scofield, 1920). All the men in the air and on the sea were searching for the bright crescent of light that would be visible during the dark of the moon (Scofield, 1924). The inner edge of the crescent would be green and the outer edge red (Daniel Miller, private communication, 19 September 1989). Once a vessel sighted the crescent of light, the entire attack fleet would employ a number of capture techniques to ensnare the prey.

This was no hunt for an enemy submarine, but the latest twentieth century technology being used in 1919 to assist fishermen off the San Diego area in locating schools of Pacific sardine, *Sardinops sagax*. Sardines were just beginning to be used by the canning industry. Sardine canning started on the US west coast in 1889 at the Golden Gate Packing Company of San Francisco (California). When the San Francisco plant closed in 1893 the equipment was sold to the Southern California Fish Company in San Diego (Thompson, 1926). This company canned sardine in oil, mustard, spices and tomato sauce in two, one, and quarter pound sizes until 1909 (Smith, 1895; Thompson, 1926).

Another cannery started producing canned sardine in 1909 at San Diego but closed in 1913. By 1915 three sardine canneries were in operation, one in San Francisco and two in Monterey. The Monterey plants commenced canning in 1902 (the Booth plant) and 1906 (Monterey Fishing and Packing Company). A San Francisco plant opened sometime between 1900 and 1915 (Schaefer et al., 1951) (Fig. 3.1). The sardine packed at the Booth plant were labeled mackerel until this practice was stopped by the US government in 1910. However, canned sardines from California soon gained a reputation for having flavor and quality equal to the then-preferred French brands.

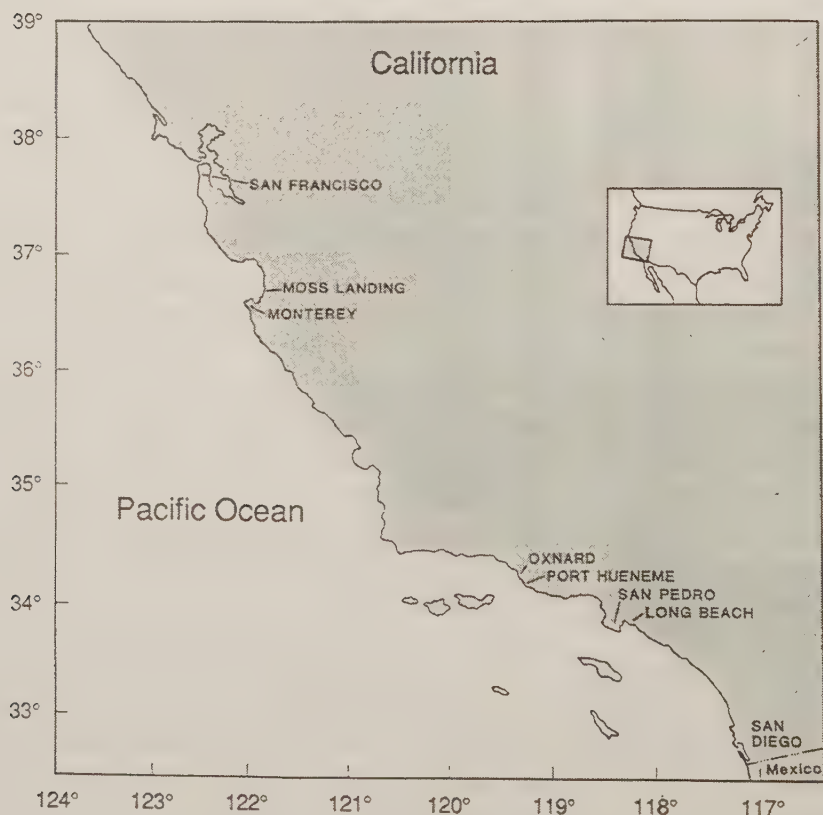


Fig. 3.1 Location of study area.

Sardine canning and reduction had become the largest fishery on the west coast by 1925. This major industry landed 173,000 tons of sardine in California and another thousand in British Columbia (Canada) during that 1925-26 season (Radovich, 1981). The sardine fishery had started out as a supplier of fresh whole fish in

the 1860s and sardines had also been used as bait since the 1880s (Smith, 1902). The shift to canning from the 1890s to the 1920s actually created two new industries. The first produced a high quality and highly valued canned sardine for human consumption; the second produced protein-rich feed for chickens as well as fertilizer for green plants. The chicken feed and the plant fertilizer were produced from canning waste, using a process called reduction. The value of this by-product soon caused canners to set up their own reduction plants at the canneries. By 1920 the increased demand for sardine meal and fertilizer resulted in some plants using whole fish along with canning waste to produce fish meal, flour, oil and fertilizer.

The California Department of Fish and Game became concerned about the direct use of sardine for nonhuman consumption in 1920. Starting in 1920, and excluding only 1923 and 1924, new laws were passed to curtail the use of whole fish for reduction in every year through 1941 (Schaefer et al., 1951). The position of the US Bureau of Fisheries was that "[canned] sardines must sell at a price that is based on their own cost of production. Production of fish meal and oil can not [sic] continue to dominate canning" (Beard, 1928). This statement was made because only plants which canned fish could legally reduce sardines: canned sardines were being produced and sold at cost or at a loss so that canneries could obtain enough waste and whole fish for reduction. Selling at or below cost kept the sales of canned sardines above what the market would have demanded. The high quality of the California canned sardine resulted in a product which could be sold in almost all existing canned sardine markets, thus increasing the sale of California sardine. The canners also received another benefit from maintaining the high quality of their canned sardines. The canning of high quality sardine produces more by-product per ton of fish landed; because there is an increase in the amount of offal and unsuitable whole fish, the assured quality is higher. This meant that more fertilizer and meal could be produced from each ton of sardine landed.

Although the state and federal governments were in agreement on the need to reserve the sardine resource for human consumption, the economics of reduction and the legal apparatus mitigated against this being accomplished. The major loophole in the legal structure existed when fish were caught and processed outside the

three-mile state jurisdiction. The inability of the state to reserve the sardine resource for human consumption became clear during the 1926–27 season, when a Monterey canner towed the concrete barge *Peralta* outside the state's three-mile jurisdiction and commenced reducing sardines, without even the pretext of canning. Because of financial, legal, and social problems, this vessel never successfully obtained sardines. A self-propelled vessel, the SS *Lake Miraflores*, also tried to obtain fish, but fishermen would not sell to her off Monterey or Santa Barbara (Fig. 3.2). The same vessel did obtain some fish off San Pedro, but the operation proved unprofitable. In November 1930 the vessel moved north to the waters just south of San Francisco; another vessel, the SS *Lansing*, joined her in 1932. These ventures became profitable and, as a result, floating reduction plants became common off all the major sardine ports from San Diego to San Francisco.



Fig. 3.2 SS *Lake Miraflores*, the first reduction ship to operate outside the jurisdiction of the State of California, unloading sardines from a purse seiner in the early 1930s (Glantz and Thompson, 1981).

Such vessels, along with a few others, operated until 1938, when oil and meal prices fell and an amendment changed the State of California's constitution. This new amendment gave the state the authority to stop offshore reduction plants. Legal proceedings were not brought to bear on these at-sea reduction plants, because the vessels had stopped processing by the time the amendment became

law. The reduction ships had landed a total of 778,560 tons of sardine in nine seasons. These nine seasons occurred during some of the best years in the sardine fishery. At-sea purchases of sardines represent an annual average of 16 percent of the sardines landed during the period.

The 1936–37 season saw the entry of Oregon and Washington into the fishery. The landings of sardine in these states, along with those in British Columbia, and California, produced the largest one-season landing of any single species of fish* ever caught on the west coast – 791,334 tons (Table 3.1).†

The 12 seasons from 1934 to 1946 would have to be considered as *pax-sardinia* in the California fishing industry. Landings averaged 599,467 tons a season. World War II prompted good prices for oil, meal, fertilizers, and canned sardine. State fishery biologists had been warning for years that the sardine biomass could not sustain removals over 250,000 tons. However, the industry and federal agencies resisted, thwarting the state biologist's attempt to enact a quota of that size, or indeed any quota at all. "The canneries themselves fought the war by getting the limit taken off fish and catching them all. It was done for patriotic reasons..." (Steinbeck, 1954).

During the next six seasons, from 1946 until 1952, landings averaged 234,068 tons. This amount was about 40 percent of the previous 12-season average. The next 10 seasons, through 1962, recorded average landings of 55,322 tons, or one-tenth the record mid-1930s to mid-1940s seasons. The last six seasons of the fishery produced average landings of 23,985 tons (Table 3.1 and Fig. 3.3). As one fisherman who participated in the last season (1968) said, "In the last year we caught them all in one night" (Louis Mascola, private communication, 6 September 1989). A fishery biologist, when asked to comment on the fishery, said that "It was big while it lasted" (Ralph Silliman, private communication, 18 September 1989).

* There are enough 10-inch sardines in these landings that together, if laid end to end, would reach from the earth to the moon and back (Reinstedt, 1978).

† During the history of this fishery, all landings were reported in short tons (908 kg). Hence the weights in this chapter have not been converted to metric units.

Table 3.1 Sardine catches from the Pacific Coast of North America (from Murphy, 1966).

Season	Pacific Northwest			California				Southern Calif.	Total Calif.	Baja Calif.	Grand Total
	British Columbia	Washing-ton	Oregon	Northern California							
				Reduction Ships	San Francisco	Monterey	Total				
1916-17						7710	19820	27530			27530
1917-18	80				70	23810	48700	72580			72660
1918-19	3640				450	35750	39340	75540			79180
1919-20	3280				1000	43040	44040	67030			70310
1920-21	4400				230	24960	25190	38450			42850
1921-22	990				80	16290	16370	36500			37490
1922-23	1020				110	29210	29320	65110			66130
1923-24	970				190	45920	46110	83930			84900
1924-25	1370				560	67310	67870	105150			174390
1925-26	15950				560	69010	69570	137270			153220
1926-27	48500				3520	81860	85380	152210			200710
1927-28	68430				16690	98020	114710	187260			255690
1928-29	80510				13520	120290	133810	220670			334990
1929-30	86340				21960	160050	182010	325170			411510
1930-31	75070			10960	25970	109620	146550	38570			260190
1931-32	73600			31040	21607	69078	121725	164645			238245
1932-33	44350			58790	18634	89599	167023	250690			295040
1933-34	4050			67820	36336	152480	256636	383429			387479
1934-35	43000			112040	68477	230854	411371	595034			638054
1935-36	45320	10	26230	150830	76147	184470	411447	149051			632058
1936-37	44450	6560	14200	235610	141099	206706	583415	726124			791334
1937-38	48080	17100	16660	67580	133718	104936	306234	416564			490404
1938-39	51770	26480	17020	43890	201200	180994	426084	575287			670557
1939-40	5520	17760	22330		212453	227874	440327	96939			582876
1940-41	28770	810	3160		118092	165698	283790	176794			493324

California

Season	Pacific Northwest				Northern California				California			
	British Columbia	Washing-ton	Oregon	Total	Reduction Ships	San Francisco	Monterey	Total	Southern Calif.	Total Calif.	Baja Calif.	Grand Total
1941-42	60050	17100	15850	93000		186589	250287	436876	150497	587373		680373
1942-43	65880	580	1950	68410		115884	184399	300283	204378	504661		573071
1943-44	88740	10440	1820	101000		126512	213616	340128	138001	478129		579129
1944-45	59120	20		59140		136598	237246	373844	181061	554905		614045
1945-46	34300	2310	90	36700		84103	145519	229622	174061	403683		440383
1946-47	3990	6140	3960	14090		2869	31391	34260	199542	233802		247892
1947-48	490	1360	6930	8780		94	17630	17724	103617	121341		130121
1948-49		50	5320	5370		112	47862	47974	135752	183726		189096
1949-50						17442	131769	149211	189714	338925		338925
1950-51						12727	33699	46426	306662	353688		353088
1951-52						82	15897	15979	113125	129104	16184	145288
1952-53							49	49	5662	5711	9162	14873
1953-54							58	58	4434	4492	14306	18798
1954-55							856	856	67090	68465	12440	80905
1955-56							518	518	73943	74461	4207	78660
1956-57							63	63	33580	33643	13655	47298
1957-58							17	17	22255	22272	9924	32196
1958-59							24701	24701	79270	103971	22334	126305
1959-60							16109	16109	21147	37256	21446	58702
1960-61							2340	2340	26538	28878	19899	48777
1961-62							2231	2231	23297	25528	21270	46798
1962-63							1211	1211	2961	4172	14620	18792
1963-64							1015	1015	1927	2942	18384	21326
1964-65							308	308	5795	6103	27120	33223
1965-66							151	151	568	719	22247	22966
1966-67							23	23	321	344	19531	19875
1967-68									71	71	27657	27728

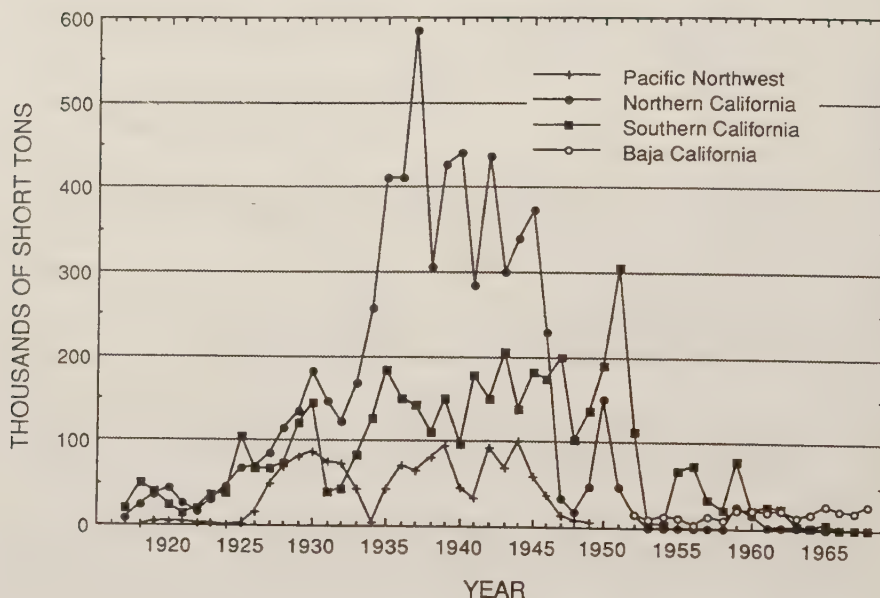


Fig. 3.3 Sardine catches from the Pacific coast of North America. Pacific Northwest includes British Columbia, Washington, and Oregon. Northern California includes reduction ships, San Francisco, and Monterey. (Data from Murphy, 1966.)

The history of the sardine fishery is not just a story of landings, government regulations and industry exploitation; nor is this story being told to affix the blame or determine the cause of the sardine fishery collapse. The causes could have been overfishing (Scofield, 1938; MacCall, 1979), management conflicts (Ahlstrom & Radovich, 1970), climate change (Smith, 1979) or, most likely, a combination of all of these.

Upon following this fishery from the 1860s to its demise in 1968, one not only becomes aware of the vast quantity of sardines harvested and the loss of a very valuable industry, but also of the people who worked in the plants, caught the fish and invested their funds in this colorful dynamic venture. The loss of the sardine industry had ramifications for the west coast fishing community, the State of California, and foreign nations in Central and South America, and Africa. The lessons available on how people, institutions, and society coped with, and learned from, this loss are every bit as important as the lessons learned from the loss of the resource itself.

The California sardine fishery was composed of the aforementioned groups of fishermen, plant workers, and entrepreneurs. These three groups of people are in no way mutually exclusive. Some fishermen and their families were involved in all three activities. Others invested and fished or invested and worked. In the very beginning in San Francisco most of the fishermen were Italian (*San Francisco Chronicle*, 20 July 1885). As the fishery moved to southern California, Portuguese and "Jugo-Slavs ('Austrian')" [sic] fishermen predominated (Skogsberg, 1925). Fishermen from Oregon and Washington in the 1930s were mostly Scandinavian. The period of expansion and large landings covered 21 years from 1925 to 1946. With one exception during that period, these nationality groupings stayed roughly the same throughout the fishing communities. In the late 1920s and 1930s Japanese-American fishermen dominated fishing for sardine out of southern California (Higgins & Holmes, 1921). At the outbreak of World War II, Japanese-American fishermen were removed to concentration camps, never to regain ownership of their vessels or their dominant position in the fishery. Beside the foregoing nationalities, two other nationalities were prominently involved as plant workers: the Mexicans and Chinese. Most of the higher skilled workforce at the plants were related to fishermen or came from the same ethnic background as the fishermen in that port.

The Monterey area, southern California, and the San Francisco area produced the majority of canned sardines and fish meal. The most famous of the sardine canning communities was, and still is, Monterey. Monterey's fame can be linked to its current tourist popularity and also to the writings of John Steinbeck, even though southern California landed as many sardines and San Francisco started earlier. The national and international distribution of the "top of the line" Monterey-canned sardines also contributed to the area's fame and recognition.

During the Great Depression (1929-41), Monterey did not suffer as much as most other areas of the US, because sardine production remained high and even increased in the late 1930s. Although the Monterey canning area became "a poem, a stink, a grating noise" to many Americans (Steinbeck, 1945), it meant bread on the table to those involved in it.

The Legaz family was one of the families that earned its livelihood from fishing. They were of Austrian decent and started their

own fishing business in 1912. In that year, with his cousins and brothers, Mr. Legaz bought a small trawler and named it the *Legaz Brothers*. The oldest of the Legaz brothers subsequently bought the *Georgia* in 1917, the *Ansonia* (70 feet – 21 m) in 1927, the *Valencia* (75 feet – 23 m) in 1928, the *Marconia* (80 feet – 25 m) in 1937, and the *Leviathan* (98 feet – 30 m) in 1946. In 1947 he invested in a sardine plant and sold out a few years later, not losing any money. His sons fished with him from age nine or ten, until they could buy their own vessels or skipper one of the other boats in the Legaz fleet. In the 1940s oil was the big moneymaker from sardines, not canning (Louis Legaz, private communication, 1 October 1989). Investing in a plant that reduced sardine was one way for fishing families to get rich.

The Legaz family was one of hundreds of families and thousands of people who fished for sardine for part of a year. A typical multi-fishery pattern consisted of fishing for salmon on the west coast of Alaska from June through September, sardine off California from October through March, and squid fishing near San Pedro and Monterey in April and May and sometimes September. The number of vessels involved in the sardine fishery was substantial. As late as 1956, the October monthly report of the Monterey office of California's Department of Fish and Game states that 150 vessels and eight airplanes were active on one night. During the 1956–57 season, landings were 33,580 tons. Each seiner and lampara vessel had between six and 10 people on board. If you expand this fishermen ratio to the *pax-sardinia* fleet of 500 vessels, then 4,000 fishermen were employed for half a year, or 2,000 fisherman-years of work annually during the 1930s and early 1940s.

The California landings in 1943 were about 500,000 tons, and in 1946 about half that amount. The ex-vessel values were US\$10.8 and US\$6.9 million, respectively (Pinsky & Ball, 1948). The product value in 1943 exceeded US\$29 million and in 1946 is estimated to have been about the same, although the 1946 catch was actually much smaller. If we expand this product value with a conservative consumer price index (CPI) to 1989, the product value would exceed US\$210 million (1946 CPI = 52, 1989 CPI = 380, 1967 CPI = 100) (Anon., 1989). Yearly employment was over 9,000 in 1946, probably far greater in 1943, and likely to have been over 25,000 in 1936, based on the relative size of the reported catches.

The wages paid to these 1943 workers was around US\$28 million, equivalent to US\$200 million in 1989 dollars.

Monterey fishermen continued to can fish until 1957, but reduction ceased by 1950. Most of the fish canned in Monterey during the 1950s were trucked in from southern California. Fishermen received an agreed-upon price regardless of the quantity landed, but had to pay the cost of trucking. The trucking rates and prices were negotiated between the union and the remaining two Monterey buyers in the late 1950s. Fishermen negotiated an ex-vessel price of US\$47.50 per ton in 1955, but after paying the cost of trucking, loading, unloading, and ice they received only US\$40.00 per ton. In August 1957 the agreed price rose US\$5.00 to \$52.50 per ton, but fishermen received US\$2.50 less, \$37.50, because the costs associated with transporting the sardines were increased to US\$15.00 per ton. In October 1957, transport costs were raised to US\$18.00, lowering the net received ex-vessel price to US\$34.50 (see the monthly California Department of Fish and Game reports for the period 1945–65). By 1960 only the bait fishery remained in Monterey, and although the ex-vessel price was sometimes US\$200 per ton, sardines were not available. Sportfishermen were paying US\$1.00 per sardine in 1968. The fishery continued in southern California until that night in 1968 when the airplanes led the fleet to the last sardine schools.

Capital formation had occurred, from 1889 to 1946, at roughly the same rate as the developing fishery. In 1946, 101 reduction plants were in operation in California. Plant ownership was distributed among a broad spectrum of people. People such as the Legaz family were only one type of owner. Other ownership structures included small investors who had combined funds. These small investors were often groups of fishermen, or cannery workers who, through investment, believed they could give themselves an opportunity to better their position by increasing job security and decreasing middleman costs. Large investors also participated. A number of investors were already wealthy, such as Zellerbach, Fleishhacker and Christopher. Christopher was mayor of San Francisco, and men like Zellerbach and Fleishhacker had friends in high local, state, and federal positions on whom they could call for help, giving these investors more political clout than the small investors. The industry was able to use this clout to

either limit laws or block (or at least postpone) effective conservation legislation.

By 1968, 80 years after the fishery had started in San Francisco, it was gone. It had collapsed, crumbled, and disappeared. The collapse had taken 22 seasons. The vessels were gone, the machinery was gone, and the people were no longer sardine workers. Fishermen had for years been witnessing the demise of the resource with fewer and smaller schools of fish almost annually. In the 1950s workers still talked about the sardines coming back. A decent season like 1958–59, when 126,000 tons were landed, would keep people hoping for another five years. Many men finally realized that the sardines would not return; the lucky or smarter fishermen went to other fields, other fisheries or other countries.

The men who had multi-fishery options diversified. Some of the smaller vessels fished market (Dungeness) crab (*Cancer magister*), from November through February, others fished rockfish (*Sebastes spp.*), albacore (*Thunnus alalunga*), and salmon (*Oncorhynchus spp.*). These vessels which changed fisheries would change from eight-man sardine crews to three- or two-man, or even skipper-only crews. The displaced crewmen found employment ashore as painters, gardeners, construction workers, and other similarly skilled positions. Many maintained their relationship with fishing by going to Alaska in the summer, but no longer fished all the year round. Those vessels which could not economically switch from lampara or seine gear fished for squid, anchovy or tuna. In the US none of the displaced fishermen or cannery workers received retraining or assistance from the government to start a new profession.

Men who owned vessels, but could no longer pay the mortgage or upkeep on their vessels, sold them. Smaller vessels, in the 45-foot range, were useful in the above-mentioned alternative fisheries. People who sold and serviced vessels, such as Woodward's in Moss Landing, saw large numbers of vessels being sold, foreclosed, not repaired, and lost at sea. Because of the large number of vessels on the market, even small vessels sold at a loss, but larger and more valuable vessels (75–110 feet – 23–33 m in length) sold for half price and even as low as 10 cents on the dollar (Lillian Woodward, vessel brokerage family, private communication, 19 September 1989). Some of these larger vessels went to Alaska to participate in the expansion of the king crab (*Paralithodes camtschatica*) fishery (see

Wooster, this volume). The low prices of the vessels kept fixed costs down, allowing new owners the luxury of learning to fish and market alternative products while having to cover little more than their operating (i.e., variable) costs.

At the same time as the vessels were being sold and transferred to other west coast fisheries, other vessels and equipment associated with sardine canning and reduction were being sold in international markets to such countries as Peru, Chile, and South Africa. Although much of the equipment pre-dated World War II, a lot of equipment was relatively new and had been used sparingly, since being purchased in the late 1940s when the fishery was in decline (Sal Ferrante, private communication, 20 September 1989).

Peru and Chile were assisted in these purchases by two agencies of the United Nations: the Food and Agriculture Organization (FAO), responsible for increasing the food (particularly protein) supply for Third World nations, and the United Nations Development Program (UNDP), responsible for securing funds for Third World development. Funds supplied by the UNDP were also used to obtain expertise in fishing, canning, reduction, and fishery management. Lampara fishermen from San Francisco and seiners from San Diego went to South America generally for six months to a year to teach fishing methods or as contract skippers. Some men sold their vessels, delivered them in South America and stayed on as skippers of the vessel. As in Alaska, the low price of idle equipment and vessels allowed the sardine and anchoveta (*Engraulis ringens*) fisheries off the west coast of South America to expand rapidly. This expansion occurred even faster, because of the technology transfer attributed to the expertise of the Californians and the low cost of equipment. Sal Ferrante, an experienced canner and reduction plant operator/owner (and other men like him), was hired to establish a new plant in Peru during the 1950s. From 1958 until 1960 he stayed on to run the plant he established. Ferrante was available to do this type of work because, in 1957, he had sold his fertilizer plant in Oxnard, California, to a South African company. The Oxnard plant was almost new and he received a good price for used sardine equipment, a price equal to about 60–70 percent of the cost of building a new facility. Ferrante's plant was dismantled, shipped to South Africa, reassembled and became operational within a matter of months. Except for the location,

nothing in the fertilizer plant had been changed, even the name on the door remained "Ferrante Co."

Other businessmen, such as Leo Hart and Craig Johnson, established companies which sold used machinery primarily to South American countries and to Mexico. Machinery was shipped to these locations from San Francisco, Moss Landing, Monterey, Port Hueneme, Long Beach, and San Diego (Fig. 3.1). Fish meal and oil reduction machinery constituted the majority of the equipment sold to South American enterprises. This equipment was generally older and less costly than the equipment shipped to South Africa. Unlike Ferrante's fertilizer plant, most equipment prices rarely exceeded half the cost of new equipment, and some were sold for one-fifth the new value. Locating these surplus machines in the western US was accomplished via a worldwide network of people who had previously worked in the production and management of California's sardine fishery.

Fishery biologists and managers from California became involved in the management of South American fisheries through the United Nations' support of Peru's Instituto del Mar (IMARPE) and the Ministerio de Comercio e Industria. Along with people from California (William Ripply and Frances Clark), Australia (Jeffery Kestevan), England (Phillip Appleyard), and other US citizens (Millian Kravanja and Wilbur Doucet), were local scientists (e.g., Coronel Portillo) attempting to evaluate the sardine and anchoveta resources of the Peru Current. Many of these people had gained knowledge and experience working with California sardine and were attempting to use that experience to manage southern clupeid stocks (William Ripply, private communication, 18 September 1989). Like the industry workers, these scientists had gone south "searching for new raw material" for their scientific skills (Popovici, 1964).

Conclusions and lessons

Global climate change is likely to cause diverse alterations and changes in fisheries around the world. Some fisheries may decline or collapse, while others may increase. The historical collapse of a major fishery like the California sardine fishery provides a number of lessons on how the local society and the national and

international fishing industry may be expected to respond to these changes.

Some of those lessons were postulated by Radovich (1981). He addressed the interactions of the politics of fishery management with the biology of the species, and concluded that "the present scarcity of sardines off the coast of California, and their absence off the northwest, is an inescapable climax, given the characteristics and magnitude of the fishery and the behavior and life history of the species" (p. 134). Lessons drawn by Radovich regarding within-fishery dynamics include the following:

- Overfishing can cause fishery collapse rather than a sustained low-level harvest.
- Political process can be controlled through industry's influence to thwart rational management.
- Development-oriented government agencies may contribute to delayed and ineffective management.
- Research can be used to delay solutions as well as to provide solutions.

We would offer a fifth lesson on the internal dynamics of fishery collapse:

- Overfishing is a natural consequence of institutional (government as well as industry) momentum, following the paradigm that "bigger is better," with size being the ultimate measure of "success."

These lessons clearly indicate the path that a new industrial clupeid fishery may be expected to take. More importantly, they indicate that strong management is necessary to counter these destructive tendencies.

New fisheries are eagerly encouraged by many segments of society, industry, and government agencies. This encouragement is often manifested in the form of subsidies:

- Non-market funding of equipment or expertise will cause the fishery to develop more rapidly than would be expected from purely market-driven development (e.g., US Navy and Coast Guard assistance in locating sardines).
- Fishery management can behave like a subsidy in that it encourages investment if its perceived presence engenders optimism, or decreased expectation of risk. In this respect, ineffective management is worse than no management at all, as

fishery development is accelerated but no resource conservation benefit is derived.

Our examination of the international events during and following the collapse of the California sardine fishery provides another set of lessons regarding the development of substitute fisheries. *A substitute fishery will develop more rapidly than would be the case for a newly developed independent fishery.* This rapid development occurs because existing capital, labor, technology, and markets are readily transferred to the substitute fishery.

- Capital, labor, and technology can be obtained at less cost and with less delay than would be required for independent development of an isolated fishery.
- Technology and expertise are available, eliminating the "learning curve."
- Labor available to substitute fisheries (semi-skilled, skilled, and managerial) has provided an opportunity to maintain preferred professional and cultural lifestyles, avoiding the economic risk and cultural hazards of retraining.
- Market development is unnecessary with substitute fisheries, because existing markets are in search of a product. Product prices offered for the substitute product are generally high.

The combination of a highly valued product due to existing unfilled market demand, subsidies, and low start-up cost (due to cheap surplus equipment and labor) provides the economic conditions for rapid industrial development. The lack of normal time delays dangerously accelerates the developmental process.

For these reasons, we expect global warming not only to cause large international relocations of fishing industries, but those relocations will be accomplished by a rapid transfer of industrial structure from collapsing fisheries to emerging or new fisheries. While both the old and new substitute fisheries may be inherently unstable because of climate change, we expect that this rapid transfer of harvesting and processing capacity will exacerbate fishery instability.

The political process of establishing management institutions and the scientific process of developing predictive fishery models are much slower than industrial development of substitute fisheries. Internationally, governments and their fishery management agencies should be prepared to adopt the politically difficult and industrially resisted management policy of deliberately con-

strained fishery development, and avoid politically popular but destabilizing subsidies. The alternative is likely to be a few years of glory and high profits followed by decades of disillusionment, unemployment and industrial decay.

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Estimates of Dolphin Abundance in the Eastern Tropical Pacific: Preliminary Analysis of Five Years of Data

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ABSTRACT

Large-scale research vessel surveys were conducted annually from 1986 through 1990 by the US National Marine Fisheries Service to monitor the abundance of dolphin populations in the eastern tropical Pacific Ocean. The species of primary interest for the surveys were dolphin stocks taken incidentally by tuna purse seiners. A stratified analysis gave estimates of abundance of nine stocks of four species (spotted, spinner, striped, and common dolphins), using line transect methods, for all five years. No significant trends in population size were detected for any dolphin stock during 1986-90, although the statistical power of detecting a trend was low.

KEYWORDS: SMALL CETACEANS; SPOTTED DOLPHIN; SPINNER DOLPHIN; STRIPED DOLPHIN; COMMON DOLPHIN; EASTERN TROPICAL PACIFIC; SURVEY - SHIPBOARD; ASSESSMENT

INTRODUCTION

Dolphins from several stocks are killed during tuna purse-seining operations in the eastern tropical Pacific (ETP). The major populations affected by the fishery are the northern offshore stock of spotted dolphins, *Stenella attenuata*, and eastern and whitebelly stocks of spinner dolphins, *S. longirostris* (Smith, 1983). Common dolphins (*Delphinus delphis*), striped dolphins (*S. coeruleoalba*), and Fraser's dolphins (*Lagenodelphis hosei*) are also taken.

In 1986, the US National Marine Fisheries Service (NMFS) initiated a long-term, large-scale research program to monitor the abundance of dolphin populations in the ETP. The program utilises two research vessels annually for 120 days each. Surveys were carried out in 1986, 1987, 1988, and 1989, and the results have been published (Holt and Sexton, 1989; 1990a; b; Gerrodette and Wade, 1991; Sexton *et al.*, 1991). In 1990, the NMFS conducted the fifth survey utilising the same vessels during the same seasons. Here we present abundance estimates for the new data from 1990, as well as for the previous four years of data, using a stratified analysis incorporating line-transect methods that differs from previous publications.

MATERIALS AND METHODS

Study area and survey methods

The surveys were designed to be replicated each year as closely as possible. The surveys covered the same areas at the same season, using the same methods, the same vessels, and even many of the same observers each year. The outside boundary of the study area was described by Au *et al.* (1979). The study area was partitioned into four areas or strata: inshore, middle, west, and south (Fig. 1). The size of each stratum was calculated by Holt and Sexton (1990b). The number of ships, the total amount of survey effort needed to achieve a given precision of estimation, and the allocation of survey effort by stratum were described in Holt *et al.* (1987).

In 1990, the NOAA research vessels *David Starr Jordan* and *McArthur* traversed randomly placed predetermined

tracklines in the ETP from 28 July through 6 December (Fig. 1). Each ship was scheduled to spend 120 days at sea, surveying tracklines similar to the previous four years. Detailed data collection procedures and data summaries for each ship are presented by Hill *et al.* (1991a; b).

Each vessel had two teams consisting of three observers each. The teams alternated watch every two hours. While on duty, two observers from the team used 25X binoculars to search from directly ahead to abeam of their respective sides of the ship. The third observer served as data recorder and searched directly ahead of the ship when not recording data. Each member of the team spent approximately equal time at each of these duty stations. Observers switched vessels at the mid-point of the cruises.

When a school was initially detected, the observers estimated the angle and radial distance to the school. When possible, schools were approached and observers recorded independent 'best' estimates of school size. When weather conditions were suitable, a Hughes 500D helicopter, based aboard the *Jordan*, was used to photograph schools whose sizes were estimated by the observers. Analyses comparing observer estimates to counts from the photographs are currently being conducted. The photographs will be used to calibrate observer estimates of school sizes.

Abundance estimation

Estimates of population abundance (N_j) of stock j were computed by line-transect methods (Burnham *et al.*, 1980) as:

$$N_j = \sum_{k=1}^4 \frac{n_{jk} f_j(0)}{2 L_k} S_{jk} A_k \quad (1)$$

where

- n_{jk} = number of schools of stock j in stratum k ,
- $f_j(0)$ = detection function of stock j evaluated at zero distance,
- S_{jk} = mean school size of stock j in stratum k ,
- L_k = total effort in stratum k in kilometres,
- A_k = total area in stratum k in square kilometres.

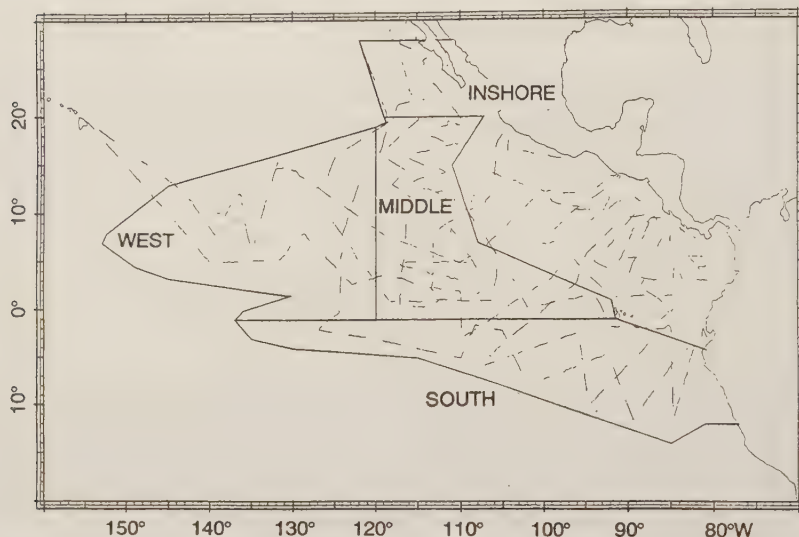


Fig. 1. Study area for the stratified survey of dolphins in the eastern tropical Pacific Ocean. Tracklines traversed while on searching effort by the NOAA vessels *David Starr Jordan* and *McArthur* during the 1990 survey are shown. Tracklines were similar in other years.

This represents a stratified analysis, where only dolphin sightings from stock j were used to calculate the density and therefore abundance of stock j within stratum k , with the abundance summed across the four strata for a total estimate for the stock.

The only exception to the stratification was the estimate of $f_j(0)$, which was based on perpendicular distances pooled across strata within a stock due to inadequate sample sizes. This resulted in only one estimate $f_j(0)$ for each stock j , and so the same estimate is used in the formula in each stratum. Some stocks had inadequate sample sizes even after pooling across strata. In such cases we also pooled across stocks within a species to obtain an adequate sample size. Details for each stock are explained below. A hazard rate model (Hayes and Buckland, 1983; Buckland, 1985) was fitted to the data to estimate $f_j(0)$.

The variance of N_j was estimated using bootstrap methods (Efron, 1982). Within each stratum, the total distance of searching effort (L_k) was tabulated, and then legs of effort were randomly selected with replacement until the amount of effort equalled L_k . This effort and the associated sightings were used to calculate $f_j(0)$, S_{jk} , n_{jk} and finally N_j . This process was repeated 200 times. The variance of N_j was calculated using these 200 estimates. A 90% confidence interval on N_j was estimated by the central 90% of the bootstrap estimates.

Data selection

Legs of effort from Beaufort states 0–5 were used, discarding a small amount of Beaufort 6 effort. Only schools detected within 7.4 km (4.0 n.miles) perpendicular distance of the trackline were used. This resulted in the elimination of approximately 2% of the sightings, depending upon stock and year, which was within the 1–3% range recommended by Burnham *et al.* (1980). A 7.4 km truncation point provided an adequate fit of the hazard model to the perpendicular distance distributions. The perpendicular distances were grouped into ten bins for the analysis, with the first four bins 0.46 km (0.25 n.miles) wide and the rest 0.926 km (0.5 n.miles) wide.

For each sighting, from one to six observers estimated school size, with the most frequent number being three. Therefore, school size estimates were averaged across observers to obtain the mean of their 'best' estimates. Sightings without any 'best' estimate of school size were not used.

Stock identification

Boundaries for each stock within the study area were described by Perrin *et al.* (1985). The current analysis used their boundaries for spotted and spinner dolphins and their recommended management unit boundaries for common and striped dolphins. The only exception, on the recommendation of Perrin *et al.* (1991), was that only one whitebelly stock was recognised rather than separate northern and southern stocks. In addition, since insufficient information existed to distinguish sightings of offshore and Baja neritic common dolphins consistently, all common dolphin sightings in the north were pooled into one estimate. This left three spotted dolphin stocks (northern offshore, southern offshore and coastal), three spinner dolphin stocks (eastern, whitebelly and Central American), three common dolphin stocks (northern including Baja neritic, central, and southern), two striped dolphin stocks (northern and southern) and one stock of Fraser's dolphins. Too few coastal spotted (14 total identified in 5 years) and Fraser's dolphin (22 in 5 years) sightings were made to estimate the abundance of those stocks. The stock of Central American spinner dolphins, previously referred to as Costa Rican spinner dolphins but recently given sub-specific status as *Stenella longirostris centroamericana* (Perrin, 1990), was not readily identified in the field. Additionally, the research vessels spent little time in its coastal stock area. No estimate of abundance was possible for this stock, as no identified sightings and few unidentified spinner sightings in the Central American stock area were made. Estimates of abundance were thus made only for the nine remaining stocks.

Stocks were based on morphological differences from the study of specimens (Perrin *et al.*, 1985; 1991), but in the field, most sightings of a species were assigned to a stock on the basis of where the sighting was made. However, some stocks of the same species overlapped geographic areas and were, under good conditions, identifiable in the field. The overlapping stocks included (1) coastal and northern spotted and (2) eastern and whitebelly spinner. On the basis of observations recorded in the field, sightings of these species were either coded as having been visually identified as of a particular stock or were recorded as being an unidentified sighting of that species. An unidentified sighting, however, could still be assigned unambiguously to a stock unless it occurred in the overlap zone between two stocks.

Therefore, unidentified spinner sightings outside of the overlap zone between the two stocks were assigned either to the eastern or whitebelly stock, depending on location. If it is assumed that the two stocks have an equal probability of being unidentified in the overlap zone, unidentified spinner sightings within the overlap zone could be allocated to the stocks by the observed ratio of the identified stocks in the overlap zone. However, there were only 2 to 4 sightings of this kind each year, so an adjustment of this type would have little effect on the total estimate of abundance. These 2–4 sightings were not used in the current analysis.

Similarly, very few (14 total in 5 years) unidentified spotted dolphin sightings were made each year in the overlap zone between the coastal and northern offshore spotted stocks. Again, a ratio adjustment based on the observed ratio of the stocks could be made, but was not in the current calculation. This represents a slight negative bias in the northern offshore, eastern spinner, and whitebelly spinner stocks, but one that should be relatively constant from year to year.

Estimates of $f(0)$ for each stock

If a stock had more than 20 sightings in each year, $f(0)$ was estimated for that stock from those sightings alone. Stocks meeting this criteria were northern offshore spotted, eastern spinner, whitebelly spinner, and southern striped. All of these stocks in fact had more than 30 sightings in each year, with the exception of the whitebelly spinner stock in 1990, which had only 24 sightings.

If a stock did not meet this criterion, perpendicular

distances were pooled across stocks of the same species to obtain an adequate sample size. None of the three common dolphin stocks met this criterion, and it was necessary to pool across all three common stocks to get enough sightings. This resulted in only one estimate of $f(0)$ for all three stocks of common dolphins.

It was also necessary to pool southern spotted sightings with northern spotted sightings to obtain a sample size large enough to estimate $f(0)$ for the southern stock. Although all northern spotted sightings could be pooled with the southern sightings, the much larger number of northern spotted sightings would make this estimate nearly identical to that of the northern stock. Therefore, only all northern spotted sightings south of 8°N were pooled with all the southern spotted sightings to estimate an $f(0)$ for the southern stock. This latitude was chosen such that the sample size criterion was met in each year.

A similar method was used for the northern striped stock. All sightings of southern striped dolphins north of 8°N, east of 130°W, and west of 95°W, were pooled with the sightings of northern striped dolphins to estimate $f(0)$ for the northern stock.

Differences in methodology from previous publications

Published estimates from the first four years of data (Holt and Sexton, 1989; 1990a; b; Gerrodette and Wade, 1991; Sexton *et al.*, 1991) used methods of estimating abundance of ETP dolphin populations that followed Holt and Powers (1982) and Holt (1987). The current analysis differs in several ways, and a summary of the main differences is presented below.

First, as described above, $f(0)$ was estimated separately for each stock rather than estimating one $f(0)$ from sightings of all dolphins, including additional species such as *Tursiops truncatus*, *Grampus griseus* and *Steno bredanensis*. Second, the previous method produced estimates of abundance for each species, and then allocated each species abundance to the stocks of the species by the ratio of the area occupied by a stock to the area occupied by the species. These areas were determined from Perrin *et al.* (1985) and were thus constant from year to year, so that estimates of abundance were completely correlated for all the stocks of a species. The current method estimated abundance for a stock, as much as possible, from just sightings of that stock. Third, the current method of analysis was stratified, as is appropriate for a stratified (unequal effort per unit area in each stratum) survey design (Burnham *et al.*, 1980).

Other differences will be mentioned here briefly. All size schools rather than only schools greater than 15 animals were used. Schools with only a 'minimum' rather than 'best' estimate of school size were not used. Unidentified dolphin schools were not included. School size was not weighted as had been previously done in some of the years. The truncation of the perpendicular distance distribution was changed from 3.7 km to 7.4 km. Bootstrap re-sampling was continued until the total distance was matched, rather than until the number of legs of effort was matched, and the number of bootstrap iterations was increased from 100 to 200.

RESULTS

According to Equation 1, estimates of dolphin abundance depended on five quantities: n_{jk} , $f_j(0)$, L_k , S_{jk} and A_k . The study area in each stratum (A_k) was fixed (Table 1). The

Table 1

Area A_k (in thousands of km², from Holt and Sexton, 1990a), percent of total study area, target distribution of percent effort (from Holt *et al.*, 1987), and achieved effort L_k in each year (in km), for a stratified survey of dolphins in the eastern tropical Pacific, 1986–90.

	Inshore	Middle	West	South	Total
Area (1000 km ²)	5,693.0	3,798.0	5,298.0	4,359.0	19,148.0
Percent of total	29.7	19.8	27.7	22.8	100.0
Target effort dist.	35.8	28.7	14.0	21.5	100.0
1986 Effort (km)	11,769.1	7,858.8	3,875.9	4,041.6	27,545.1
Percent	42.7	28.5	14.1	14.7	100.0
1987 Effort (km)	11,176.5	7,983.4	3,558.6	3,881.6	26,600.1
Percent	42.0	30.0	13.4	14.6	100.0
1988 Effort (km)	8,932.9	6,079.6	3,209.0	5,053.4	23,274.8
Percent	38.4	26.1	13.8	21.7	100.0
1989 Effort (km)	10,907.2	7,446.9	3,527.5	4,777.4	26,659.1
Percent	40.9	27.9	13.2	17.9	100.0
1990 Effort (km)	10,031.2	8,945.4	5,599.2	6,669.2	31,245.0
Percent	32.1	28.6	17.9	21.3	100.0

Table 2

Number of school sightings (n_{jk}), school encounters per 1000km ($1000 \cdot n_{jk}/L_k$) and mean school size (S_{jk}) for each stock in each stratum and year.

	Inshore	Middle	West	South	Total		Inshore	Middle	West	South	Total
a. 1986						c. 1988					
<i>Number of school sightings (n_{jk})</i>						<i>Number of school sightings (n_{jk})</i>					
N. Offshore spotted	69	32	17	0	118	N. Offshore spotted	54	18	13	0	85
S. Offshore spotted	0	0	0	5	5	S. Offshore spotted	0	0	0	5	5
Eastern spinner	41	15	3	1	60	Eastern spinner	33	4	0	0	37
Whitebelly spinner	7	12	10	5	34	Whitebelly spinner	2	10	21	4	37
N. Common	11	0	0	0	11	N. Common	8	0	0	0	8
C. Common	10	0	1	0	11	C. Common	19	1	1	0	21
S. Common	4	4	0	12	20	S. Common	0	12	0	15	27
N. Striped	18	20	0	0	38	N. Striped	20	3	0	0	23
S. Striped	52	25	7	12	96	S. Striped	80	23	19	38	160
<i>School encounters per 1000km ($1000 \cdot n_{jk}/L_k$)</i>						<i>School encounters per 1000km ($1000 \cdot n_{jk}/L_k$)</i>					
N. Offshore spotted	5.9	4.1	4.4	0.0	4.3	N. Offshore spotted	6.0	3.0	4.1	0.0	3.7
S. Offshore spotted	0.0	0.0	0.0	1.2	0.2	S. Offshore spotted	0.0	0.0	0.0	1.0	0.2
Eastern spinner	3.5	1.9	0.8	0.2	2.2	Eastern spinner	3.7	0.7	0.0	0.0	1.6
Whitebelly spinner	0.6	1.5	2.6	1.2	1.2	Whitebelly spinner	0.2	1.6	6.5	0.8	1.6
N. Common	0.9	0.0	0.0	0.0	0.4	N. Common	0.9	0.0	0.0	0.0	0.3
C. Common	0.8	0.0	0.3	0.0	0.4	C. Common	2.1	0.2	0.3	0.0	0.9
S. Common	0.3	0.5	0.0	3.0	0.7	S. Common	0.0	2.0	0.0	3.0	1.2
N. Striped	1.5	2.5	0.0	0.0	1.4	N. Striped	2.2	0.5	0.0	0.0	1.0
S. Striped	4.4	3.2	1.8	3.0	3.5	S. Striped	9.0	3.8	5.9	7.5	6.9
<i>Mean school size (S_{jk})</i>						<i>Mean school size (S_{jk})</i>					
N. Offshore spotted	86.9	89.6	86.0	0.0	87.5	N. Offshore spotted	176.5	112.5	210.0	0.0	168.1
S. Offshore spotted	0.0	0.0	0.0	234.1	234.1	S. Offshore spotted	0.0	0.0	0.0	173.7	173.7
Eastern spinner	105.2	78.3	119.5	44.3	98.1	Eastern spinner	214.8	61.0	0.0	0.0	198.2
Whitebelly spinner	100.8	55.3	119.4	68.4	85.4	Whitebelly spinner	352.2	41.3	99.6	292.2	118.4
N. Common	223.6	0.0	0.0	0.0	223.6	N. Common	1083.2	0.0	0.0	0.0	1083.2
C. Common	185.8	0.0	26.0	0.0	171.3	C. Common	516.8	58.0	98.0	0.0	475.0
S. Common	554.0	182.7	0.0	412.6	394.9	S. Common	0.0	330.6	0.0	780.1	580.3
N. Striped	38.5	17.5	0.0	0.0	27.4	N. Striped	80.8	101.0	0.0	0.0	83.4
S. Striped	49.5	67.8	57.3	33.4	52.8	S. Striped	71.3	56.0	57.3	84.2	70.5
b. 1987						d. 1989					
<i>Number of school sightings (n_{jk})</i>						<i>Number of school sightings (n_{jk})</i>					
N. Offshore spotted	61	46	16	0	123	N. Offshore spotted	72	29	14	0	115
S. Offshore spotted	0	0	0	12	12	S. Offshore spotted	0	0	0	6	6
Eastern spinner	37	14	1	0	52	Eastern spinner	51	11	1	0	63
Whitebelly spinner	1	16	17	6	40	Whitebelly spinner	3	12	11	5	31
N. Common	3	1	0	0	4	N. Common	7	2	0	0	9
C. Common	14	2	2	0	18	C. Common	7	0	0	0	7
S. Common	3	0	0	5	8	S. Common	7	7	0	12	26
N. Striped	5	11	0	0	16	N. Striped	21	24	0	0	45
S. Striped	86	29	5	23	143	S. Striped	62	20	8	27	117
<i>School encounters per 1000km ($1000 \cdot n_{jk}/L_k$)</i>						<i>School encounters per 1000km ($1000 \cdot n_{jk}/L_k$)</i>					
N. Offshore spotted	5.5	5.8	4.5	0.0	4.6	N. Offshore spotted	6.6	3.9	4.0	0.0	4.3
S. Offshore spotted	0.0	0.0	0.0	3.1	0.5	S. Offshore spotted	0.0	0.0	0.0	1.3	0.2
Eastern spinner	3.3	1.8	0.3	0.0	2.0	Eastern spinner	4.7	1.5	0.3	0.0	2.4
Whitebelly spinner	0.1	2.0	4.8	1.5	1.5	Whitebelly spinner	0.3	1.6	3.1	1.0	1.2
N. Common	0.3	0.1	0.0	0.0	0.2	N. Common	0.6	0.3	0.0	0.0	0.3
C. Common	1.3	0.3	0.6	0.0	0.7	C. Common	0.6	0.0	0.0	0.0	0.3
S. Common	0.3	0.0	0.0	1.3	0.3	S. Common	0.6	0.9	0.0	2.5	1.0
N. Striped	0.4	1.4	0.0	0.0	0.6	N. Striped	1.9	3.2	0.0	0.0	1.7
S. Striped	7.7	3.6	1.4	5.9	5.4	S. Striped	5.7	2.7	2.3	5.7	4.4
<i>Mean school size (S_{jk})</i>						<i>Mean school size (S_{jk})</i>					
N. Offshore spotted	86.9	134.0	102.4	0.0	106.5	N. Offshore spotted	127.7	190.9	170.9	0.0	148.9
S. Offshore spotted	0.0	0.0	0.0	149.3	149.3	S. Offshore spotted	0.0	0.0	0.0	273.8	273.8
Eastern spinner	76.1	206.7	84.2	0.0	111.4	Eastern spinner	121.8	163.1	100.3	0.0	128.7
Whitebelly spinner	572.9	94.1	58.8	171.7	102.7	Whitebelly spinner	124.0	101.7	303.1	279.4	204.0
N. Common	98.0	47.0	0.0	0.0	85.3	N. Common	341.6	50.0	0.0	0.0	276.8
C. Common	314.4	33.5	93.0	0.0	258.6	C. Common	196.0	0.0	0.0	0.0	196.0
S. Common	241.7	0.0	0.0	132.6	173.5	S. Common	418.1	384.9	0.0	652.8	517.5
N. Striped	34.0	31.4	0.0	0.0	32.2	N. Striped	37.9	34.7	0.0	0.0	36.2
S. Striped	53.6	49.4	49.6	90.3	58.5	S. Striped	45.0	64.0	57.5	116.4	65.6

[Continued]

Table 2 (continued)

	Inshore	Middle	West	South	Total
e. 1990					
<i>Number of school sightings (n_{jk})</i>					
N. Offshore spotted	66	36	11	0	113
S. Offshore spotted	0	0	0	8	8
Eastern spinner	30	12	1	0	43
Whitebelly spinner	4	6	10	4	24
N. Common	6	1	0	0	7
C. Common	14	1	0	0	15
S. Common	1	2	0	10	13
N. Striped	12	7	1	0	20
S. Striped	51	33	17	18	119
<i>School encounters per 1000km ($1000 \cdot n_{jk}/L_k$)</i>					
N. Offshore spotted	6.6	4.0	2.0	0.0	3.6
S. Offshore spotted	0.0	0.0	0.0	1.2	0.3
Eastern spinner	3.0	1.3	0.2	0.0	1.4
Whitebelly spinner	0.4	0.7	1.8	0.6	0.8
N. Common	0.6	0.1	0.0	0.0	0.2
C. Common	1.4	0.1	0.0	0.0	0.5
S. Common	0.1	0.2	0.0	1.5	0.4
N. Striped	1.2	0.8	0.2	0.0	0.6
S. Striped	5.1	3.7	3.0	2.7	3.8
<i>Mean school size (S_{jk})</i>					
N. Offshore spotted	124.6	147.9	89.5	0.0	128.6
S. Offshore spotted	0.0	0.0	0.0	199.9	199.9
Eastern spinner	113.6	64.5	31.2	0.0	98.0
Whitebelly spinner	90.4	62.0	75.2	534.3	150.9
N. Common	130.4	14.0	0.0	0.0	113.8
C. Common	172.2	165.0	0.0	0.0	171.8
S. Common	500.0	315.5	0.0	557.9	516.1
N. Striped	69.3	24.9	22.0	0.0	51.3
S. Striped	40.9	62.7	76.9	86.6	59.0

other quantities varied each year and are summarised in Tables 1-3 for the years 1986-1990. Each of these other quantities is discussed briefly below.

The survey employed a stratified design based on the densities of northern offshore spotted dolphins (Holt *et al.*, 1987). Although we attempted to keep the number of trackline miles searched within each stratum (L_k) a constant proportion of the total effort each year (target effort distribution in Table 1), the achieved percent effort

varied somewhat by year due to mechanical breakdowns, variations in weather and difficulties in securing permits to conduct the surveys within the territorial waters of some countries (Table 1). Total trackline effort within the study area in conditions of Beaufort 5 or less was about 27,000km annually (range 23,275 to 31,245).

The number of sightings of dolphin schools (n_{jk}) of stocks numerous enough to make abundance estimates totalled about 350 annually (Table 2). Northern offshore spotted and southern striped dolphins were the most frequently sighted schools each year. Some stocks, for example, southern offshore spotted dolphins, consistently had few sightings. The rate of dolphin school encounters per 1000km reported in Table 2 is a relative measure of dolphin school density each year; it is not used in Equation 1 to estimate abundance but is given here for comparative purposes. The number of school sightings is multiplied by mean school size (S_{jk}) for each stock in each stratum to obtain an estimate of the number of dolphins seen. Mean school size varied considerably by stratum and year. Common dolphins tended to have the largest school sizes of the species reported here.

The fitting of a probability density function to the sighting data was the most difficult part of the analysis, and variability in this parameter appeared to contribute most to the bootstrap variance of the total population estimate. Additionally, the estimates of $f_j(0)$ varied substantially among years for some of the stocks (Table 3). As noted above, there were too few sightings to form reliable estimates of $f_j(0)$ by stratum, so data were pooled and a single $f_j(0)$ is reported for each stock j . For common dolphins, stocks also had to be pooled and a single value is given for the species. The number of sightings on which each estimate of $f_j(0)$ was based is also shown in Table 3.

These quantities were combined in Equation 1 to give estimates of dolphin abundance for each stock in each year (Table 4). The coefficient of variation for the abundance estimate of northern offshore spotted dolphins, the stock for which the surveys were designed, varied from 0.25 to 0.36; CVs for other stocks were generally higher. Annual changes in abundance are shown graphically in Fig. 2a-d.

DISCUSSION

The estimated number of dolphins of each stock in each year as reported in Table 4 and shown in Fig. 2a-d should be regarded as provisional estimates subject to further analysis. Ongoing work at the Southwest Fisheries Science Center is attempting to address the direction and magnitude of any potential sources of bias in these estimates. Some potential sources of bias are listed below.

- (1) The proportion of schools detected on the trackline may be less than the assumed 1.0, which would result in a negative bias. However, an independent observer experiment in 1990 suggested that no large schools were missed on the trackline. If small schools were infrequently missed, the bias would be small.
- (2) The estimate of mean school size may be positively biased because of the decreased probability of detection of smaller schools at greater perpendicular distances from the trackline. Our preliminary investigations have indicated an increasing trend in mean school size as the truncation point is increased, confirming that a positive bias of approximately 5-20% in mean school size exists, depending on the stock.

Table 3

Estimated detection function evaluated at zero distance ($f_j(0)$) and the number of sightings used to make the estimate (n), for each stock in each year.

		1986	1987	1988	1989	1990
N. Offshore spotted	$f_j(0)$	0.67	0.73	0.69	0.66	0.31
	n	118	123	85	115	113
S. Offshore spotted	$f_j(0)$	0.69	0.88	0.42	1.12	0.31
	n	40	53	33	39	39
Eastern spinner	$f_j(0)$	0.70	0.56	0.60	0.64	0.63
	n	60	52	37	63	43
Whitebelly spinner	$f_j(0)$	0.98	1.24	1.00	0.67	0.54
	n	34	40	37	31	24
N. Common	$f_j(0)$	1.21	0.51	0.85	1.35	1.46
	n	47	30	57	46	37
C. Common	$f_j(0)$	1.21	0.51	0.85	1.35	1.46
	n	47	30	57	46	37
S. Common	$f_j(0)$	1.21	0.51	0.85	1.35	1.46
	n	47	30	57	46	37
N. Striped	$f_j(0)$	1.48	0.60	0.98	0.82	0.73
	n	45	36	51	59	43
S. Striped	$f_j(0)$	0.74	0.84	0.79	1.05	0.96
	n	96	143	160	117	119

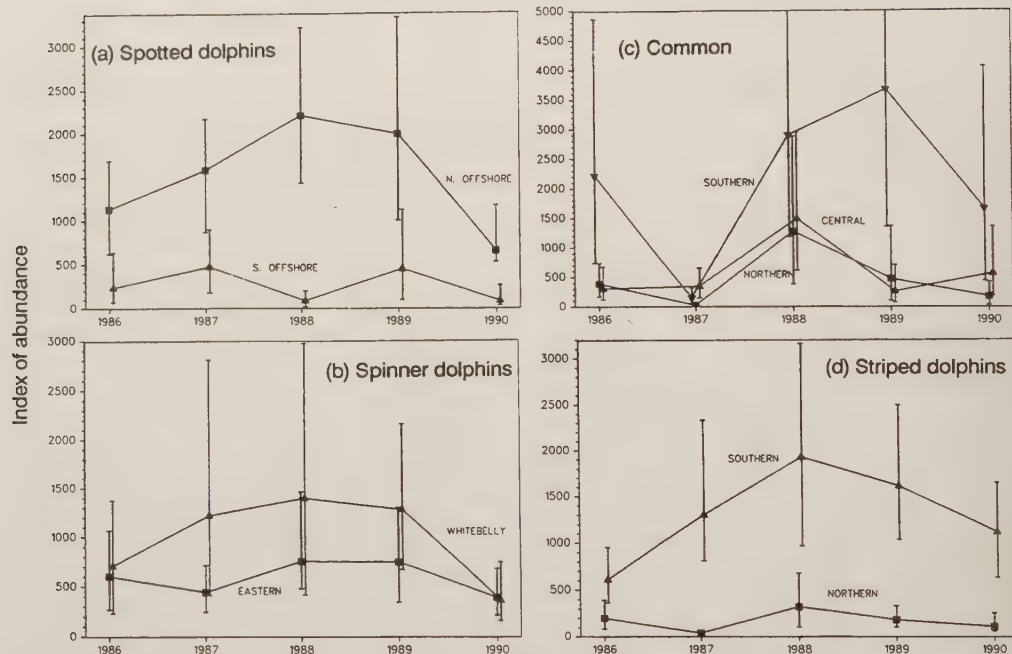


Fig. 2. Annual estimates of abundance for: (a) two stocks of spotted dolphins; (b) two stocks of spinner dolphins; (c) three stocks of common dolphins; and (d) two stocks of striped dolphins. Error bars are 90% bootstrap confidence limits.

Table 4

Abundance estimates N , (in thousands), standard errors (SE), and coefficients of variation (CV) for estimates of 9 stocks of eastern tropical Pacific dolphins, 1986-90.

	1986	1987	1988	1989	1990
N. Offshore Spotted	1,134.2	1,582.6	2,205.5	1,993.6	658.3
SE	346.5	402.8	575.1	720.7	195.2
CV	0.305	0.255	0.261	0.362	0.297
S. Offshore Spotted	236.0	475.8	85.8	451.9	87.7
SE	175.4	230.0	58.2	346.0	75.6
CV	0.743	0.483	0.678	0.766	0.863
Eastern Spinner	603.7	444.7	754.2	748.8	391.2
SE	286.1	146.0	327.9	318.8	163.6
CV	0.474	0.328	0.435	0.426	0.418
Whitebelly Spinner	706.1	1,220.7	1,398.4	1,280.0	363.3
SE	371.1	786.7	777.6	486.1	201.0
CV	0.526	0.644	0.556	0.380	0.553
N. Common	390.0	23.5	1,272.4	473.6	177.7
SE	192.4	18.2	921.7	345.5	128.7
CV	0.493	0.773	0.724	0.730	0.724
C. Common	306.2	348.1	1,487.6	261.0	568.0
SE	216.1	152.6	775.2	218.4	383.5
CV	0.706	0.438	0.521	0.837	0.675
S. Common	2,217.3	152.0	2,896.5	3,664.0	1,657.5
SE	1,525.3	85.1	1,712.0	2,601.5	1,147.9
CV	0.688	0.560	0.591	0.710	0.693
N. Striped	201.1	40.7	323.4	185.2	111.6
SE	108.6	15.2	180.5	76.5	69.2
CV	0.540	0.373	0.558	0.413	0.620
S. Striped	612.0	1,300.8	1,927.9	1,611.4	1,115.6
SE	174.2	454.2	685.3	485.4	309.7
CV	0.285	0.349	0.355	0.301	0.278

- (3) These different probabilities of detecting large and small schools, while affecting the estimate of mean school size, should not bias the estimate of school density, as long as the estimator is pooling robust, as it should be (Burnham *et al.*, 1980).
- (4) The estimate of mean school size may also be biased due to errors by the observers in estimating school size. However, aerial photography during the surveys has shown that, on average, observers estimated school size accurately, although for the largest schools there was a tendency to underestimate school size.
- (5) A negative bias in the estimation of $f(0)$ may also result from pooling sightings across strata, as the stratum with the most effort (the inshore stratum) had the lowest average Beaufort sea state, and therefore the better sighting conditions.
- (6) Reaction of the dolphins to the ship before detection could lead to a negative bias if they avoided the ship or a positive bias if they were attracted to the ship. To be a significant bias, dolphin schools would have to perceive and react to the ship at a large distance, because the average detection distance from the ship was approximately 5km. Aerial observations on a limited number of dolphin schools have shown that some dolphin schools turn away from the ship at more than this distance, but that most schools are detected by observers before they react to the ship (Au and Perryman, 1982; Hewitt, 1985). Therefore, ship avoidance behaviour by the dolphins probably results in a small negative bias in the estimates presented here.
- (7) Unidentified dolphin sightings were not used in the current analysis, creating a negative bias. However,

assignment of those sightings to dolphin stocks would only increase the abundance estimates slightly, because the number of unidentified dolphins seen was less than 3% of the total number of dolphins seen during the study, and such schools were often far from the trackline.

Thus, some of these potential biases are positive and a few more are negative. Although there is still uncertainty in many of them, none appears to have a large effect. In such circumstances, these estimates would be fairly close to absolute estimates of abundance.

In addition, a large amount of information has been collected during the five years about the habitat where the dolphins were seen (Fiedler *et al.*, 1990; Reilly, 1990). A canonical correspondence analysis indicates that much of the interannual variability in species composition can be accounted for by two multidimensional axes of environmental variables (Reilly and Fiedler, 1990). Further work will attempt to use observed changes in dolphin habitat in the ETP to help explain changes in estimates of abundance.

The estimates of abundance in Table 4 differ from reports of previous years' surveys (Holt and Sexton, 1989; 1990a; b; Gerrodette and Wade, 1991) due to different methods of analysis. As noted in Methods, previous analyses pooled data over strata, stocks, and species before estimating $f(0)$ and S , then allocated total abundance according to various estimated proportions. The present analysis avoids pooling insofar as possible. The resulting stratified analysis gives less precise, but also less biased estimates of dolphin abundance. Work on improving the analysis is continuing.

The estimates of abundance shown in Fig. 2a-d are highly variable, and it is difficult to discern any common pattern. There is no overall declining trend during the five-year study period, as might be expected if mortality due to the tuna purse-seine fishery in the ETP were having a strong impact on the populations. However, the data also do not warrant any conclusion that no impact is occurring, because the statistical power of detecting even a large decline during a five-year period given the observed variability of the estimates is low (Gerrodette, 1987).

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EVIDENCE THAT FIN WHALES RESPOND TO THE GEOMAGNETIC FIELD DURING MIGRATION

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Summary

We challenge the hypothesis that fin whales use a magnetic sense to guide migration by testing for associations between geophysical parameters and the positions where fin whales were observed over the continental shelf off the northeastern United States. Monte Carlo simulations estimated the probability that the distribution of fin whale sightings was random with respect to bottom depth, bottom slope and the intensity and gradient of the geomagnetic field. The simulations demonstrated no overall association of sighting positions with any of these four geophysical parameters. Analysis of the data by season, however, demonstrated statistically reliable associations of sighting positions with areas of low geomagnetic intensity and gradient in winter and fall, respectively, but no association of sighting positions with bathymetric parameters in any season. An attempt to focus on migrating animals by excluding those observed feeding confirmed the associations of sighting positions with low geomagnetic intensity and gradient in winter and fall, respectively, and revealed additional associations with low geomagnetic gradients in winter and spring. These results are consistent with the hypothesis that fin whales, and perhaps other mysticete species, possess a magnetic sense that they use to guide migration.

Introduction

Because little is known about how some marine animals navigate over long distances, it is necessary to identify environmental stimuli that animals might use to guide their movements in the deep ocean (Harden Jones, 1968). Many of the stimuli commonly considered to provide directional and positional information are unavailable to marine animals travelling in the deep ocean because (1) the animals

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do not possess the necessary sensory modality (e.g. olfaction in cetaceans), (2) the sensory modality exists but does not exhibit the sensitivity necessary to provide useful information to the animal [e.g. temperature sensitivity in tuna (Steffel *et al.* 1976)], or (3) the stimulus is out of sensory contact (e.g. bottom topography in the deep ocean). One possible stimulus is the geomagnetic field, which provides a great deal of stable positional and directional information (Skiles, 1985), although behavioral evidence for any ability of animals to detect the geomagnetic field has been sparse and poorly documented until only recently.

During the last twenty years, laboratory orientation and conditioning experiments have demonstrated that many migratory and homing animals respond to the direction or some feature related to the intensity of the geomagnetic field, or to both of these parameters. For example, migratory birds placed in featureless arenas exhibit preferences for orientation in seasonally appropriate directions that can be controlled experimentally by systematic variation of magnetic field direction (Wiltschko, 1972; Emlen, 1975), and fish (Kalmijn, 1981; Walker, 1984) and honeybees (Walker and Bitterman, 1985, 1989a,b; Walker *et al.* 1989) have been conditioned to respond to a variety of different magnetic field stimuli. In addition, involvement of magnetic field stimuli in pigeon homing has been demonstrated by comparing the homing performance of pigeons with magnets or coils mounted on their heads with that of control birds (Keeton, 1971, 1972; Walcott and Green, 1974) or by releasing the birds at local geomagnetic field anomalies (Walcott, 1978). These results have led to renewed interest in the hypothesis that animals use the geomagnetic field to guide their long-distance movements, particularly where they cannot use other stimuli.

An important step towards indirectly demonstrating the operation of a magnetic sense in cetaceans was taken by Klinowska (1985), who reasoned that otherwise healthy whales that strand themselves alive must have made a serious navigational mistake and that analyzing the circumstances surrounding such strandings might identify the sensory modality responsible for the error. After she had plotted live stranding positions on magnetic field maps of the coast of Great Britain, Klinowska (1985) observed an association between stranding positions and areas where magnetic minima intersect the coast, and suggested that cetaceans possess a magnetic sensory system. Kirschvink and his colleagues (Kirschvink *et al.* 1986; Kirschvink, 1990) extended Klinowska's work. They mapped stranding positions from a computerized data set onto digital aeromagnetic data for the east coast of the United States and then developed procedures that demonstrated statistically reliable associations of stranding sites with locations where magnetic minima intersected the coast. Total intensity variations of as little as 50 nanoTesla (nT; 0.1 % of the total field) were sufficient to influence stranding location (Kirschvink *et al.* 1986; Kirschvink, 1990).

If a magnetic sense is used by whales at sea to guide their migrations, it should be possible to demonstrate evidence of differential responses to the geomagnetic field. The assumption of such correlative studies is that responses by the animals to important environmental stimuli, including the geomagnetic field, should be

detectable as statistical associations of sighting positions with spatial variations in the properties of the stimuli. It is necessary to use a statistical approach in order to overcome the difficulty that the geomagnetic field is but one of many physical and biological stimuli, and there is no way to recognize or measure behavioral responses to the field by individual animals.

To test for geomagnetic sensitivity in whales, we needed rigorously collected sighting position data for a species that undertakes regular migrations in an area for which there are sufficient magnetic and bathymetric data. We obtained a computerized data set recording the positions where fin whales were observed at sea during dedicated aerial surveys together with digital geomagnetic and bathymetric data for the coast and continental shelf of the northeastern United States. We then did Monte Carlo simulations to test the null hypothesis that the whale positions were random with respect to geomagnetic and bathymetric parameters. Subsequent simulations tested whether there was any temporal pattern to the associations that could be related to known migratory behavior. Our results suggest that fin whales recognize and associate with geomagnetic field features independently of other geophysical stimuli and that their association with geomagnetic field features is correlated with seasonal migration patterns.

Data and methods

Sighting data

The Cetacean and Turtle Assessment Program (CETAP) was sponsored by the Bureau of Land Management and conducted between October 1978 and January 1982 by the University of Rhode Island in outer continental shelf (OCS) waters of the northeastern United States from Cape Hatteras, North Carolina, to the Gulf of Maine and from shore to 9.3 km (5 nautical miles) seaward of the 1829 m (1000 fathoms) isobath. Population surveys were conducted by CETAP to assess the distribution and abundance of whales, dolphins and sea turtles inhabiting the OCS. Each survey flew a series of parallel aerial transects selected randomly from a pool of lines running northwest-southeast and spaced at 3.7 km (2 nautical mile) intervals. Observers on the surveys collected both meteorological and behavioral observations, the latter involving identifying, counting and recording positions and making notes on the behavior of the whales and other animals observed during the flights. The entire CETAP data base included nearly 70 000 entries and 112 variables. (For a more complete description of the data and methods of collection employed see Kenney and Winn, 1986.)

Geophysical data

The magnetic anomaly data were obtained in high-density gridded digital format from the Geological Society of North America's Decade of North American Geology (DNAG) program. The DNAG data set, which is distributed by the NOAA Geophysical Data Center, includes all the CETAP study area. The survey also covers most of the North American continent and extends over the Atlantic

and Pacific Oceans. Using the new Definitive Geomagnetic Reference Field, the data were compiled and merged at different levels from the following sources: original shiptrack data, flight line data, gridded data and compiled regional maps. All data are in Universal Transverse Mercator coordinates and are gridded at 2 km intervals. All the magnetic intensity data were given a positive offset to produce net values of field intensity that were positive and would fit in two bytes of memory (integer $\times 2$) on a micro-VAX II computer system.

The intensity data then were mapped onto a 512 $\times$ 512 array of picture elements (pixels). The field gradient at each point in the array was determined by calculating the mean difference between the field intensity at each pixel and the intensity at each of the eight adjacent pixels. The gradient data were then mapped onto the array and plotted as the image shown in Fig. 1, with the gradient at each pixel being assigned a color shade ranging from blue (lowest) to yellow (highest).

A similar procedure was followed with bathymetric data for the region taken from the Digital Bathymetric Data Base, which we obtained from the National Geophysical Data Center. Using this data set, which contains over 7.8×10^6 data values on a 5' (0.083°) grid, we were able to assign a value for the bottom depth to each pixel in the array. The bottom slope at each pixel was calculated in the same way as the magnetic field gradient was calculated from the magnetic intensity data. We were thus able to produce pixel by pixel matches to the geomagnetic data for two bathymetric parameters over the CETAP study area and to prepare images of bathymetric parameters like those produced for the magnetic data (Fig. 1; Kirschvink *et al.* 1986).

Biological and geophysical constraints on the study area

The key conclusions of the CETAP study for our work were that the Gulf of Maine is an important summer feeding area for mysticete whales, and that several mysticete species migrate there during spring from winter habitats in the deep ocean or to the south of the Gulf of Maine (Kenney and Winn, 1986). Little is known about mysticete migration patterns except that the whales generally spend winter in breeding grounds in low latitudes, move north (in the northern hemisphere) to higher latitudes during spring and summer to enter feeding grounds, and return south to lower latitudes during fall (Gaskin, 1976). Of species observed in the CETAP surveys, only the fin whales were observed outside the Gulf of Maine in numbers large enough for analysis. Migration through the area south of the Gulf of Maine could be inferred only from latitudinal shifts in peak abundance of sightings in different seasons (Winn and Edel, 1982). Other mysticete species were usually first seen entering the Gulf of Maine and made little use of the continental shelf and slope between Cape Hatteras and Cape Cod (Kenney and Winn, 1986). A variety of odontocete species, such as pilot whales, that were common in the CETAP area were excluded from the study because they gave no evidence of migration (Winn and Edel, 1982) or were associated primarily with the continental margin and slope rather than with the continental shelf (see below).

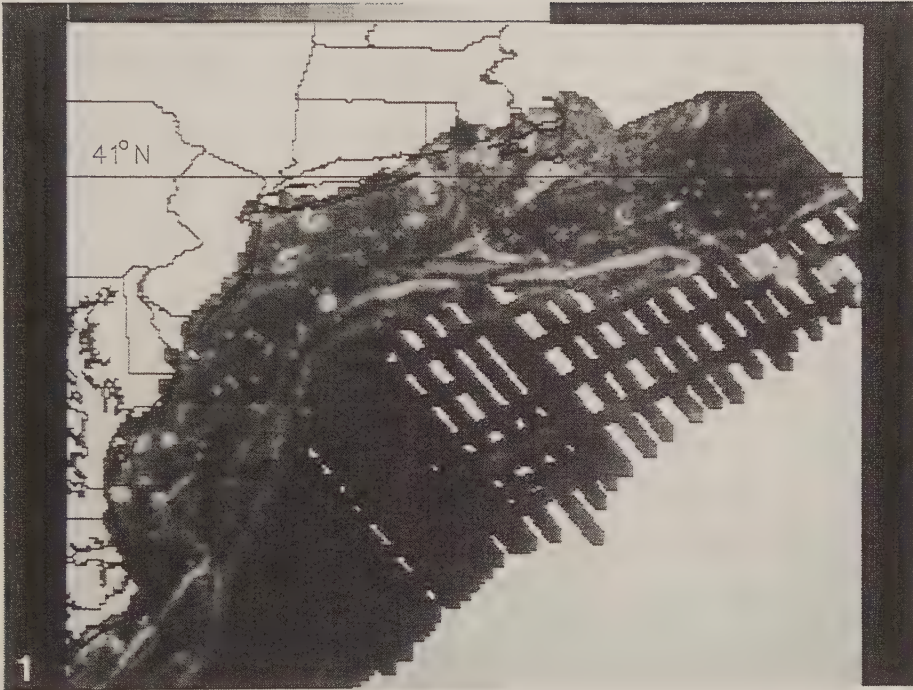


Fig. 1. Sighting positions (all seasons) for fin whales superimposed on an image of magnetic field intensity gradients over the outer continental shelf off the northeastern United States. Magnetic data are from the DNAG data set. Sighting positions from the CETAP dedicated aerial surveys are indicated by red crosses. Magnetic field gradients are indicated by shading, with 256 steps between minimum (blue) and maximum (yellow) gradients. The dark east-west line indicates latitude 41°N.

The areas covered by the geophysical and sighting data sets and the uses made by fin whales of different parts of the CETAP study area placed two important constraints on our study. First, magnetic and bathymetric data are correlated where the continental margin (indicated by the East Coast Magnetic Anomaly running parallel to the coastline in Fig. 1; see also Fig. 1 of Kirschvink *et al.* 1986) and continental slope (182.9–1829 m depth) coincide. Second, the Gulf of Maine is a summer feeding ground for mysticete whales (Kenney and Winn, 1986), which means that the distribution of sightings was highly likely to be controlled by the distribution of prey organisms. Fin whale sightings in the Gulf of Maine were aggregated and the animals were often observed feeding. By contrast, sightings in the area south of the Gulf of Maine could be treated as independent of each other because the observed frequencies of sightings per pixel gave a variance to mean ratio of 1.062 and fitted expected Poisson frequencies (goodness of fit $\chi^2_2=3.47$, $P>0.1$; Pielou, 1969). Feeding by fin whales was observed only rarely outside the Gulf of Maine. We therefore restricted our analyses to testing for associations of sightings with geomagnetic and bathymetric parameters over the continental shelf (<182.9 m depth) south of 41°N , which we used to mark the southern limit of the Gulf of Maine.

Monte Carlo simulations

We did Monte Carlo simulations to test the hypothesis that fin whale sighting positions in the southern region of the CETAP study area were associated with one or more of the geophysical parameters (geomagnetic field intensity and gradient; bottom depth and slope). The simulations were made by generating a set of random sighting positions along each CETAP flight track. Each track received the same number of observations as was present in the original CETAP survey and, where flight tracks passed outside the boundaries of the study area, the number of positions assigned was reduced to match the number of real positions found within the study area. The means and variances of magnetic field intensity, magnetic field gradient, depth and bottom slope for the simulated positions were then computed and the results from 1000 or more such simulations compared with those obtained from the original data. A mean value for any of the geophysical parameters at real sighting positions that was greater (or less) than 975 out of 1000 mean values for simulated positions gave a two-tailed probability of 0.05 that the sighting positions were non-randomly associated with the geophysical parameter.

In subsequent simulations, we partitioned the sighting data to test for the influence of season and behavior on associations of sighting positions with geophysical parameters. We did simulations after sorting the data by calendar months (trimesters) corresponding to the seasons: winter was December–February, spring was March–May, summer was June–August and fall was September–November. We then did simulations in which the data were sorted by season and behavior. Animals observed feeding or in behavior associated with feeding were excluded from the simulations on the assumption that the positions where such animals were observed would be controlled by the distribution of their

prey organisms. Final sample sizes resulting from these treatments ranged from 7 (fall) to 31 (spring) per trimester for fin whales sighted in the study area.

Results

The Monte Carlo simulations made with all sightings included (summarized in Table 1) demonstrated no overall association of fin whale sighting positions with any geophysical parameter tested. Monte Carlo simulations (summarized in Table 2A) testing for the influence of season on the distribution of sighting positions with respect to the four geophysical parameters, however, demonstrated a series of associations of fin whale sighting positions with geomagnetic but not with bathymetric parameters. Sighting positions were associated with areas of high geomagnetic field gradient ($P=0.02$) during summer but low intensity in winter ($P=0.02$) and low gradient in fall ($P=0.008$).

Further simulations (summarized in Table 2B) in which animals observed feeding were excluded from the analysis demonstrated associations of sighting positions only with low geomagnetic gradients and intensity. The simulations for the fall trimester were not affected because no animals were observed feeding. The new simulations also had little effect on the result for geomagnetic intensity in winter ($P=0.034$) as only one animal had been excluded. After exclusion of feeding animals, the simulations demonstrated further associations of sightings with low geomagnetic field gradients in the spring ($P=0.024$) and winter ($P=0.038$) trimesters but, again, no association of sighting positions with bathymetric parameters. In contrast, exclusion of a single observation of feeding removed the significant association of sighting positions with areas of high geomagnetic field gradient during summer.

Table 1. *Results of Monte Carlo simulations used in two-tailed tests of the hypothesis that the mean values of the geophysical parameters at positions where fin whales were sighted were significantly different from the mean values of the parameters at simulated sighting positions on the CETAP flight tracks*

Parameter	N	Mean actual positions	Mean simulated positions	P
Bottom depth	94	58.4	58.5	0.638
Bottom slope	94	298.6	316.5	0.346
Field intensity	94	1841.1	1858.8	0.068
Field gradient	94	110.7	120.7	0.700

Mean values for each parameter at actual and simulated sighting positions are shown in the middle columns of the table.

N, number of sightings.

Probabilities (P) given in the right-hand column of the table are that the mean values of the geophysical parameters for the simulated positions that are equal to or lower than the mean values for the parameters at actual sighting positions could be obtained by chance.

Table 2A. Results of Monte Carlo simulations used in two-tailed tests of the hypothesis that the mean values of the geophysical parameters at positions where fin whales were sighted in different seasons were significantly different from the mean values of the parameters at simulated sighting positions on the CETAP flight tracks

Parameter	All	Winter	Spring	Summer	Fall
Number of sightings	94	16	41	30	7
Bottom depth	0.638	>0.1	>0.1	>0.1	>0.1
Bottom slope	0.346	>0.1	>0.1	>0.1	>0.1
Field intensity	0.068	0.020	>0.1	>0.1	>0.1
Field gradient	0.700	0.092	0.088	>0.1*	0.008

*The mean value for magnetic field gradient at sighting positions in summer was higher than would have been expected from chance ($P=0.02$).

The probabilities for all seasons combined are the same as those in the last column of Table 1.

B. Results of simulations made with animals observed feeding or in behavior associated with feeding excluded from the analysis

Parameter	All	Winter	Spring	Summer	Fall
Number of sightings	82	15	31	29	7
Bottom depth	>0.1	>0.1	>0.1	>0.1	>0.1
Bottom slope	>0.1	>0.1	>0.1	>0.1	>0.1
Field intensity	>0.1	0.034	>0.1	>0.1	>0.1
Field gradient	>0.1	0.038	0.024	>0.1	0.008

Cells in the table contain estimates of the probabilities that the mean values of the geophysical parameters for the simulated positions that are equal to or lower than the mean values for the parameters at actual sighting positions could be obtained by chance.

Frequency histograms of the values for the magnetic field intensity and magnetic field gradient at pixels on the tracks flown by the CETAP in the winter, spring and fall are plotted in Fig. 2A–D. Pixels in which fin whales were sighted are indicated by the shaded portions of the histograms and represent only a very small proportion (1–2 %) of the total sample of pixels in all seasons except for the fall. Evidence that pixels containing whale sightings comprise a non-random subset of the pixels on the flight tracks would be expected to appear as a displacement of each distribution above or below the distribution for all pixels.

The patterns of the distributions shown in Fig. 2 are consistent with the results of the Monte Carlo simulations. The medians and arithmetic means of the distributions of pixels with whales all occurred at lower values than did those of the distributions for pixels on the flight tracks. For example, the arithmetic mean value for magnetic intensity for pixels with whales was approximately 100 nT lower than for all pixels on the flight tracks in winter (Fig. 2A). Similarly, the arithmetic mean values for magnetic gradient for pixels with whales were between 25 % and 45 % (30–40 units) below the mean gradient values for all pixels on the flight tracks

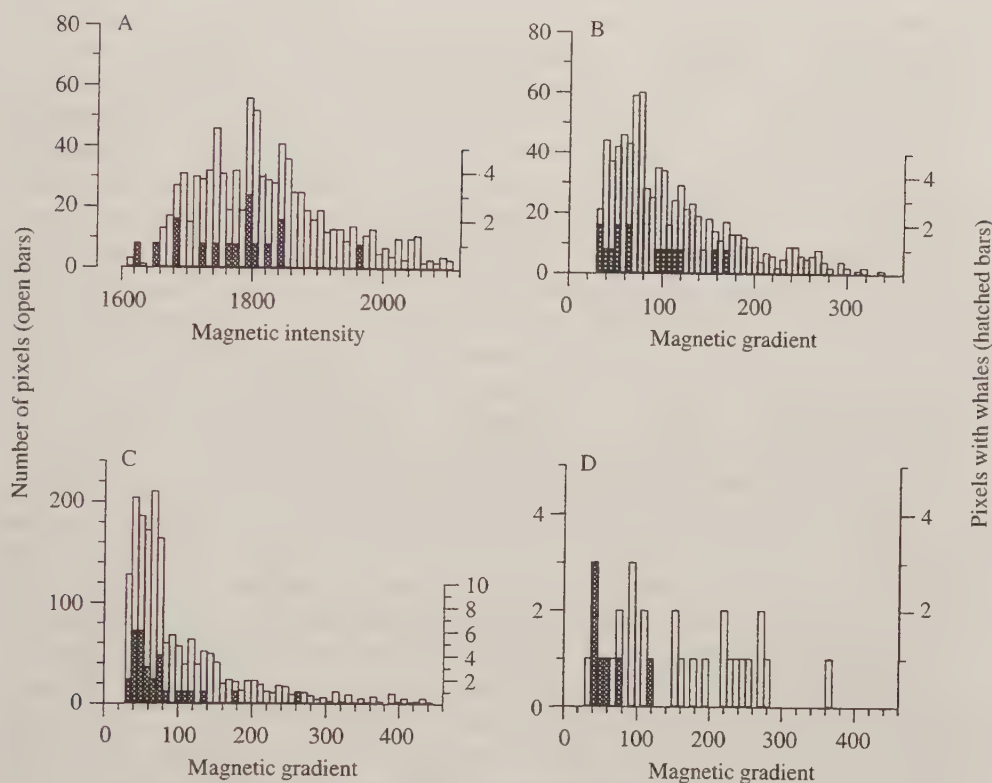


Fig. 2. Frequency distributions of (A) geomagnetic field intensity at pixels lying along all the tracks flown in winter in the study area; (B–D) geomagnetic field gradient at pixels lying along all the tracks flown in winter (B), spring (C) and fall (D) in the study area. The shaded portions of the histograms indicate (on the scale shown on the right-hand ordinate) the distribution of values of the parameters at the pixels in which non-feeding fin whales were observed.

in winter, spring and fall (Fig. 2B–D). As might be expected from the results of the simulations, the distributions of the pixels containing whales were also truncated at high values. In the four frequency histograms in Fig. 2, no more than one pixel with whales was observed in the upper half of the range of each histogram where at least 2–5 would have been expected if sightings had been randomly distributed with regard to the geomagnetic parameters.

Discussion

Although there was no previous experimental evidence for magnetic sensitivity in whales, our results are consistent with the hypothesis that fin whales possess a magnetic sense and that they use it to travel in areas of low geomagnetic field gradient and possibly low magnetic intensity during migration. We began our

study with the most straightforward analysis possible with our data – using all sightings of fin whales made by the CETAP in the area south of 41°N – and proceeded to more complex analyses in which we sorted the sighting data by season and behavior. The study showed (1) that the positions in the study area for fin whales not seen actively feeding were associated statistically with areas of low geomagnetic field gradient and (2) that these associations were correlated with the general pattern of the northward and southward migrations undertaken during spring and fall, respectively, by mysticete whales (Gaskin, 1976; Winn and Edel, 1982). Additional associations of the sightings with areas of low magnetic field intensity and gradient were demonstrated in winter. Taken together, these findings are consistent with earlier analyses of live strandings of whales, which showed that strandings occur most often in areas where magnetic minima – areas characterized by low magnetic field gradients and intensities – intersect the coast (Klinowska, 1985; Kirschvink, 1990; Kirschvink *et al.* 1986). The data used in this study, however, were free of the sampling biases to which the stranding data were subject (Mead, 1979) and reflected behavior in normal, rather than abnormal, situations.

It is worth noting that five of the 32 simulations gave statistically reliable evidence of association of sightings with geophysical parameters where no more than two would have been expected from chance and that all of the associations demonstrated were with magnetic field parameters. All of the tests were two-tailed and were made on the only species observed in the CETAP surveys for which we were able to test the sighting data. These observations make it highly unlikely that the positive results from our simulations could be statistical artifacts or could have arisen through chance.

We consider it unlikely that similar analyses would have demonstrated significant associations of sightings with other environmental stimuli that might guide migration by fin whales. No associations between sightings of any species of mysticete whales and other environmental stimuli were found in early studies that would indicate use of the stimuli to guide migration (reviewed in Dawbin, 1966). Although Winn and Edel (1982) reported associations between bathymetric parameters and positions for mysticete whales sighted in the Gulf of Maine during the CETAP surveys, no such associations were detected outside this area.

Although there is still no experimental evidence for a magnetic sense in whales, our results are consistent with a variety of experimental results from other species. For example, Walcott (1978) released homing pigeons at local geomagnetic field anomalies and found that the more complex the pattern of magnetic field intensity gradients on the route home, the more scattered were the bearings at which the birds vanished from view at the release site. In addition, spatial variations or gradients in magnetic field intensity and a requirement that the animals be moving appeared to have been responsible for discrimination in recent magnetic conditioning experiments with both tuna (Walker, 1984) and honeybees (Walker and Bitterman, 1985, 1989a,b; Walker *et al.* 1989).

Several possibilities for experimental study arise from this work. First, although

the transduction mechanism for responses to geomagnetic fields has yet to be identified, an obvious candidate is the particles of single-domain magnetite detected in the anterior dura mater of the humpback whale, *Megaptera novaeangliae* (Fuller *et al.* 1985). A magnetite-based system is the only one yet proposed for cetaceans that could provide the sensitivity necessary to permit detection of fluctuations in the geomagnetic field as low as 100 nT (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985; Yorke, 1981). Second, a number of species, such as pilot whales, which figured prominently in the stranding studies (Klinowska, 1985; Kirschvink, 1990; Kirschvink *et al.* 1986), can be maintained in captivity. Behavioral experiments testing for response to magnetic field stimuli therefore may be possible with these species.

Such studies present formidable obstacles. As a consequence, we expect that correlation studies will be the only practical means available in the near future to test the hypothesis that cetaceans respond to the geomagnetic field. Kirschvink (Kirschvink *et al.* 1986; Kirschvink, 1990) has advanced the hypothesis that following magnetic minima may be a useful strategy for guiding long-distance movements. A prediction of this hypothesis is that, during north-south migrations in the deep ocean, mysticete whales should be observed more frequently over the magnetic minima formed by seafloor spreading than elsewhere. This prediction could be tested by survey and tracking studies over the deep ocean along the paths between the summer feeding and wintering grounds used by mysticete whales. It may be possible also to investigate associations of sighting positions with the geomagnetic field for odontocete whales over the deep ocean or in areas where the continental slope is not marked by a salient magnetic anomaly. One such area is the continental slope and deep ocean off the Pacific coast of the United States. Problems for such a study will be the limited movements of most odontocete species and the difficulty of identifying feeding animals. Until such surveys are made, work similar to ours can be done using presently available geomagnetic and sighting data sets. Such studies need not be confined to whales as similar data exist for sea turtles, other marine mammals and birds and can benefit from the methods developed thus far.

There is, therefore, a developing body of evidence that cetaceans possess a magnetic sense that they use to guide movement. Our study differed from the earlier stranding studies because we were able to test whether point values of the geomagnetic field intensity and gradient influenced the distribution of sightings, whereas the stranding studies tested whether measures of the 'shape' of the field along the coast influenced the distribution of strandings. The results obtained using the two types of measure were, however, quite similar to each other and also to field experiments with homing pigeons and conditioning experiments with fish and honeybees. We suggest that our approach may be useful for studying the contribution of a magnetic sense to the guidance of homing and migration in a variety of species.

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PROTEOLYSIS OF SKELETAL MUSCLE IN YELLOWFIN TUNA (*THUNNUS ALBACARES*): EVIDENCE OF CALPAIN ACTIVATION

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Abstract—1. White muscle of yellowfin tuna is subject to a form of deterioration known as "burnt tuna".

2. TEM and SDS-PAGE were used to quantify cellular differences in deteriorated white muscle of yellowfin tuna.

3. Electron micrographs showed a significant loss of Z-disc integrity and an increase in intracellular edema in burnt tuna.

4. Electrophoresis established that a specific doublet of proteins, 42 kD and 46 kD was lost.

5. Proteolysis of isolated myofibrils incubated in calpain (EC 3.4.22.17) was greatest at pH 7.5 and was selective for intermediate molecular weight proteins.

6. This evidence suggests that burnt tuna is a specific and limited proteolysis of myofibrillar structural proteins characteristic of calpain proteolysis.

INTRODUCTION

"Burnt tuna" is the term used by fishermen and commercial buyers to describe white muscle of yellowfin tuna (*Thunnus albacares*) that appears pale, grainy, exudative and unacceptable for the sashimi market (i.e. raw consumption). Since this muscle deterioration first appears *post mortem* and progresses for hours afterwards it is not considered a muscle disease but instead a breakdown of metabolic or proteolytic regulation associated with death. Burnt tuna appears in approximately 25% of the tuna caught by commercial handliners in Hawaii (Bourke, 1985) and elsewhere (Gibson, 1981) producing real economic losses to the sashimi fishery. Besides the clear monetary motive for identifying the cause of burnt tuna, it affords an opportunity to examine the control of muscle proteolysis.

Sport-caught fish and those landed by the night handline fishery put up a fierce struggle during capture. Since burnt tuna occurs more often in fish captured by these procedures, struggling has been presumed to contribute to its cause. Tuna white muscle has extraordinarily high lactate dehydrogenase activity (LDH) and produces some of the highest muscle lactate concentrations found in nature (Guppy and Hochachka, 1978). Therefore, high lactic acid concentrations and low muscle pH were once thought to be responsible for burnt tuna (Konagaya and Konagaya, 1978). However, failure to find a close correlation between pH and burnt tuna (Cramer *et al.*, 1981) or products of acid-mediated proteolysis (Hochachka and Brill, 1987) led to the formulation of

new theories regarding the etiology of this muscle degeneration. Hochachka and Brill (1987) and later Watson *et al.* (1988) proposed an alternate hypothesis, that burnt tuna was caused by a calcium activated neutral proteinase (calpain) which cleaved structural proteins within muscle fibers rather than the contractile proteins.

While these theories were consistent with what was known about burnt tuna, they were untested. The purpose of this investigation was to evaluate the hypothesis that burnt tuna was the result of calpain proteolysis. This was done by quantifying the micro-anatomical and biochemical differences between burnt and unburnt muscle in whole *post mortem* tuna to determine their consistency with calpain proteolysis. Also, yellowfin tuna held in captivity were used to directly assess the effects of exhaustive exercise and calpain treatment on tuna muscle. In brief, this study was designed to answer several questions: (1) How does burnt tuna differ from other tuna microanatomically and biochemically? (2) Can burnt tuna be caused by severe exercise alone? and (3) Is it merely an accelerated *post mortem* generalized proteolysis or is it a specific proteolysis consistent with what is known of calpain?

MATERIALS AND METHODS

Sample collection

For analysis of ultrastructure of normal muscle, small (~2 kg) wild yellowfin tuna were caught at sea, stunned by a blow to the head and muscle samples taken by needle biopsy.

Changes in muscle structure caused by severe exercise alone were examined using captive yellowfin tuna held at the Kewalo Research Facility (Honolulu Laboratory, National Marine Fisheries Service, Honolulu, U.S.A.). Individual fish were dip netted from their holding tanks, biopsied and quickly moved to a doughnut shaped tank. The fish were

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then chased to exhaustion, sacrificed by a blow to the head, and the muscle biopsied immediately.

Sampling of yellowfin tuna at the Honolulu Fish Auction is complicated by uncontrollable variables such as sex of the fish, fight time, vigorousness of the capture struggle, time of year, and the nutritional state of the animal at the time of hooking, as well as a variety of *post mortem* treatments administered before the fish reaches the auction. Therefore, all samples taken from a commercial fish auction were from partially burnt fish so each animal acted as its own control for these variables.

Yellowfin tuna judged to be burnt by the wholesale buyers at the United Fishing Agency Honolulu Fish Auction (Honolulu, U.S.A.) were sampled for electron microscopy and SDS-PAGE. The judgment of the buyers was based on a visual analysis of flesh quality from quartered fish. Three paired biopsies were taken from areas judged to be completely burnt and adjacent areas that were designated as totally unburnt (saleable for sashimi). Tissue was immediately placed in buffered fixative for microscopy. Similarly paired biopsies from ten yellowfin tuna were collected for SDS-PAGE. 400 mg samples were sealed in polyethylene tubes, immediately placed on dry ice, and stored in a -90°C freezer until electrophoresis.

Post mortem age is also unknowable in auction sampled yellowfin tuna. To record *post mortem* changes in vigorously exercised, large (>40 kg) fish, needle biopsies were taken from sport-caught yellowfin tuna at the Kona Hawaii Billfish and the Hawaiian International Billfish Tournaments. Samples were obtained as soon as the fish were brought to the dock in Kailua-Kona (Hawaii) and at intervals until the time of sale. The time of death of tournament-caught fish is recorded, and all biopsies were taken at known *post mortem* intervals which could be compared to samples from auction sampled fish.

Electron microscopy

Muscle was placed in either 0.15 M phosphate buffered fixative, 0.15 M sodium cacodylate buffered fixative or 0.2 M sodium cacodylate buffered fixative, each containing 2.5% glutaraldehyde. Samples were secondarily fixed in 2% osmium tetroxide plus 0.08% potassium ferrocyanide. After secondary fixation, samples were dehydrated and embedded in LX112 resin. Thin sections were cut with a diamond knife, mounted on 200 mesh unsupported copper grids, and stained with saturated uranyl acetate in water followed by Reynolds' lead citrate (Reynolds, 1963). Sections were viewed and photographed using a Philips 300 electron microscope set at 60 kilovolts.

Analysis of ultrastructural quality

At least four blocks were prepared from each biopsy and two blocks per biopsy were thin-sectioned longitudinally. From each of these blocks, 25 thin sections were cut and mounted on to 5 copper grids. One of these grids was chosen at random to be viewed under the electron microscope. The first grid square encountered that contained tissue was photographed in its entirety at a magnification of $3200\times$. Sixteen to 30 negatives were made from each grid square (depending upon the amount of overlap), developed and printed at a standard size of 8×10 . Montages were then created.

A test grid of 88 squares was overlaid on the montage. Ten squares were chosen at random, and the Z-discs within that square were categorized: (1) = Z-disc completely intact, (2) = Z-disc with one hole only, (3) = Z-disc with multiple holes, (4) = Z-disc position identified only by I bands, (5) = No Z-disc position identifiable.

The test grid was moved to an adjacent area until the entire montage was covered. Z-discs from the montage were then summed by category.

Numbers of Z-discs from burnt tuna micrographs were pooled by condition category for all three fish. The same was

done for unburnt samples. Since categories 1-3 represented existing Z-discs these data were pooled by cell and this total used for *F*-tests, paired *t*-tests and analysis of variance (ANOVA) to determine differences in the number of Z-discs/cell between burnt and unburnt tuna.

The volume of intracellular edema, as a percentage of cell volume, was measured using point analysis and the same 88-square test grid. Edema was calculated as a percentage of total cell volume. Mean percentage of edema for each cell was analyzed by *F*-test. The limit for statistical significance was $P < 0.05$.

Sodium dodecyl-sulfate-PAGE

Samples were prepared from 100 mg of either burnt or unburnt muscle in 4 ml of homogenizing buffer (in mM: 100 KCl, 1 EDTA, 50 imidazole, 5 mercaptoethanol, pH 7.5). Tissues were homogenized by four 10 sec bursts at 70% speed in a Tissumizer tissue grinder and then centrifuged at 800 g for 15 min. Aliquots of the supernatant and homogenate were prepared for electrophoresis as per Laemmli (1970). Samples were placed on a 5% stacking gel over a 10% separating gel, electrophoresed and stained overnight with 0.1% Coomassie Blue R250 (Sigma, St Louis, MO) made up in 10% acetic acid and 50% methanol. Destaining was done with 7% acetic acid. Molecular weight of proteins was estimated by relative mobility using known molecular weight compounds electrophoresed simultaneously as standards. Gels were analyzed by densitometry to determine the quantity of individual muscle proteins remaining in burnt and unburnt tuna.

Preparation of isolated myofibrils

Myofibrils were prepared from captive yellowfin tuna according to the method of Etlinger and Fischman (1973) except for the elimination of 0.02% deoxycholate in one wash and the use of three washes instead of ten. The purity of the prepared myofibril fraction was verified by TEM and light microscopy. Preparations that contained only myofibrils (i.e. no whole cells or membrane fragments) were placed in a solution of 100 mM KCl, 0.25 mM thioglycolic acid and 50% glycerol (Reddy *et al.*, 1983) stored in a -20°C freezer.

Incubation of myofibrils

Calpain was purchased from Sigma and kept at -20°C until it was used. It was then thawed and diluted 1 unit/ml, with enzyme buffer (in mM: 20 Tris, and 1 EDTA, pH 7.5). All proteinase used was from the same lot number. The ratio of calpain/myofibrils was 1:100 w/w.

Myofibrils were incubated (at 25°C) at three pHs (5.5, 6.8 and 7.5) using a buffer modified from Reddy *et al.* (1983). The only changes were an increase in CaCl_2 from 1 mM to 5 mM and an increase in myofibrillar concentration from 1 mg/ml to 5 mg/ml. The reaction volume was 1 ml. Reactions were stopped at 10 min intervals by the addition of 125 μl of 10% TCA. After a 10 min centrifugation at 14,000 g the supernatant was withdrawn and the absorbance measured at 280 nm in a Beckman Model 35 Spectrophotometer to determine the quantity of acid-soluble peptides released from the myofibrils. Absorbance readings from five to seven myofibril incubations at each pH were averaged and regression lines calculated. Pellets were prepared for SDS-PAGE.

RESULTS

Electron microscopy

Auction sampled yellowfin tuna. Morphological preservation in 0.2 M (i.e. 400 mOsm) sodium cacodylate buffer was slightly better than with the other concentrations of fixatives. There was less swelling of the sarcoplasmic reticulum (SR) and

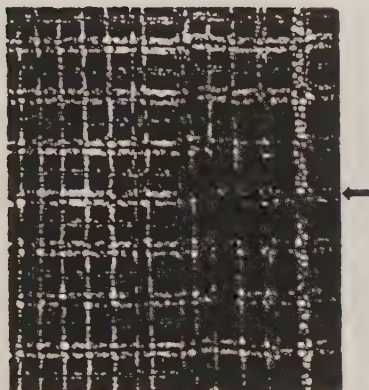


Fig. 1. White muscle from a small (<2 kg), wild yellowfin tuna biopsied immediately *post mortem*. The animal was captured by hook and line and quickly brought to the boat with a minimal amount of struggling. Note the integrity of the Z-discs (arrow indicated Z-disc) and the absence of intracellular edema. Mag. 8300 $\times$.

slightly less disruption of the mitochondria in the 400 mOsm buffer with no deterioration in the quality of myofibrillar fixation.

An electron micrograph of white muscle from wild yellowfin tuna is shown in Fig. 1. The salient features of this normal muscle are the integrity of the Z-disc and the absence of intermyofibrillar space. In contrast, burnt tissue sampled at the Honolulu Fish Auction (Fig. 2) exhibits Z-disc disintegration or even absence, and relatively large spaces between myofibrils, indicative of edema. The unburnt cells from the same fish (Fig. 3) more closely resemble myofibrils from freshly caught, wild tuna. Note that the Z-discs are present, but that a few holes indicate some limited proteolysis. Some intracellular edema also is evident, but it is much less than in burnt muscle. Samples taken from a yellowfin tuna judged to be completely

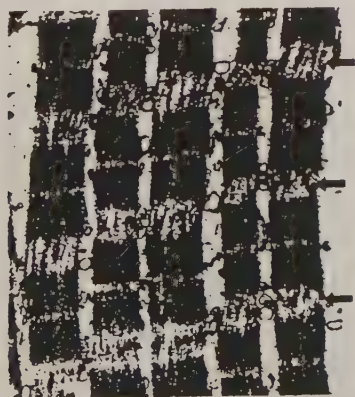


Fig. 2. White muscle sampled from a yellowfin tuna at the Honolulu Fish Auction. The sample was taken from an area of muscle judged to be severely burnt. Note the Z-discs (arrows indicate Z-disc position) show significant deterioration. 17,000 $\times$.

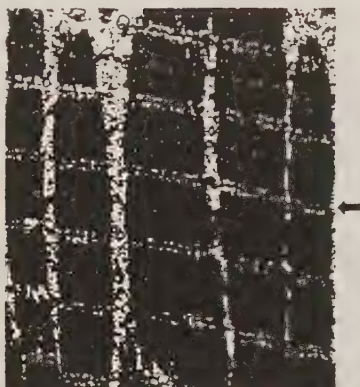


Fig. 3. White muscle from the same fish as in Fig. 2. This sample was taken from an area of muscle judged to be unburnt. The Z-discs have some holes (arrow indicated Z-disc position), but are largely intact. 17,000 $\times$.

unburnt show the same degree of Z-disc integrity as unburnt tuna (Fig. 4).

Significantly more Z-discs were present in unburnt cells (*F*-test). Z-discs/cell in unburnt and burnt cells from the same fish also were significantly different (paired *t*-test). A significant difference in the number of Z-discs/cell existed between burnt and unburnt cells for all three fish (ANOVA). The ANOVA used to test the hypothesis that the reduction in Z-disc number seen in burnt tuna is uniform across fish showed no significant differences between burnt cells in any of the fish sampled. Since burnt cells from different fish were more similar than burnt and unburnt cells from the same fish, the data from all three fish were pooled. Figure 5 shows the percentage of Z-discs/condition category. Muscle tissue classified as burnt clearly has significantly more disorganized Z-discs (categories 3-5) than tissue classified as unburnt. Mean percentage of edema was also significantly greater in burnt than in unburnt yellowfin tuna cells (*F*-test). In summary, burnt yellowfin tuna tissue exhibited more edema and fewer Z-discs per cell than unburnt tissue.



Fig. 4. White muscle from a yellowfin tuna judged to be 100% unburnt. 17,000 $\times$.

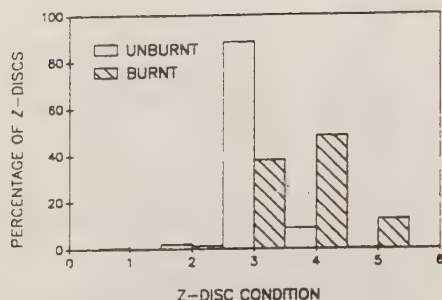


Fig. 5. Frequency histogram of Z-disc condition in burnt and unburnt muscles from fish sampled at the Honolulu Fish Auction.

Exercised yellowfin tuna. Of the three captive fish exercised to exhaustion and sacrificed only one had any myofibrillar disorganization and it was unrelated to that seen in burnt tuna. The muscle fibrils were torn mid-A band (Fig. 6). Some mechanical stress of swimming appears to have caused this rending of the myofibrils while leaving the Z-discs undisturbed. These results show that burnt tuna is not the direct result of mechanical disruption due to severe exercise. While exercise can cause major myofibrillar changes in muscle, it alone does not cause disruption that resembles burnt tuna.

Post mortem deterioration. All 8 *post mortem* samples taken from tournament-caught yellowfin tunas showed muscular changes similar to those in auction sampled unburnt tuna. A typical muscle fiber (Fig. 7), taken 16 hr *post mortem* had only minimal Z-disc damage. Despite intense exercise white muscle from these yellowfin tunas remained unburnt long after death, that is, it was saleable as sashimi and retained the Z-disc in muscle ultrastructure.

Is burnt tuna the unavoidable result of *post mortem* deterioration? In other words, given sufficient time i.e. more than 16 hr, will all muscle eventually become



Fig. 6. Myofibrils taken immediately *post mortem* from a yellowfin tuna exercised to exhaustion. Note that myofibrils are torn at mid-A band but that the Z-discs are intact (arrow indicates Z-disc position). 17,000 $\times$.



Fig. 7. White muscle sample taken from a yellowfin tuna caught using sportfishing gear during the Hawaiian International Billfish Tournament. Note that even after severe exercise during capture, the muscle showed little Z-disc damage 16 hr *post mortem* (arrow indicates Z-disc position). 17,000 $\times$.

burnt? A yellowfin tuna sampled 21 days *post mortem* had no more Z-disc damage (Fig. 8) than muscle 16 hr old (Fig. 7) despite advanced *post mortem* age and decayed appearance of the flesh. Since burnt tuna is not inevitable, it is probably the result of a specific proteolytic cascade rather than an accumulated general auto-digestion.

Sodium dodecyl sulfate-PAGE

Auction sampled yellowfin tuna. SDS-PAGE analysis showed no discernible difference in the amount of alpha-actinin in burnt and unburnt tissue. This was unexpected considering the Z-disc disintegration seen in the electron micrographs. However, as shown in Fig. 9, a doublet of proteins (42 and 46 kD) is missing in burnt tuna, both from supernatant and homogenate preparations.

Ten paired biopsies were taken from auction sampled yellowfin tuna white muscle and the tissue supernatant electrophoresed on PAGE gels. Analysis by densitometry showed that the 42,000 and 46,000 Da proteins were both significantly diminished

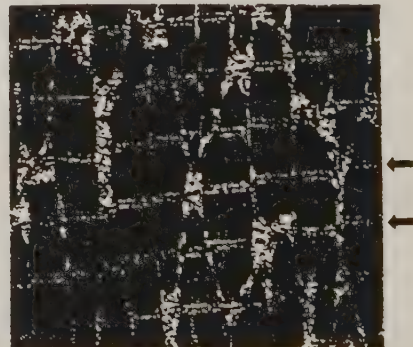


Fig. 8. Yellowfin tuna sampled at the Honolulu Fish Auction >21 days *post mortem*. Note that the muscle still had intact Z-discs despite the extreme decay (arrows indicate Z-disc positions). 16,000 $\times$.

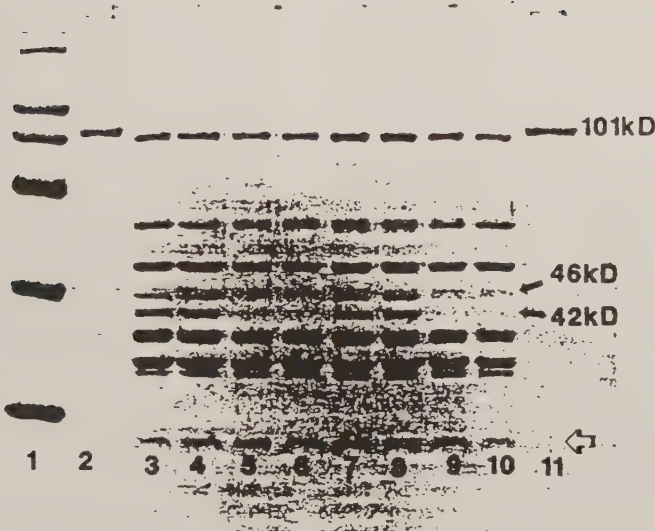


Fig. 9. Polyacrylamide gel of paired burnt and unburnt samples from two yellowfin tuna. Lane 1: High molecular weight standard, lane 2: alpha-actinin standard lanes 3, 4, 7, 8: supernatant of unburnt muscle, lanes 5, 6, 9, 10: supernatant of burnt muscle, lane 11: alpha-actinin standard. Note the missing doublet of proteins (46 and 42 kD) in burnt muscle samples.

in burnt tuna in comparison with unburnt tuna ($P < 0.05$).

Myofibril incubation with calpain. Myofibrils incubated at pH 7.5 with purified calpain demonstrated a faster rate of proteolysis than those incubated at more acidic pHs (Fig. 10). Electrophoresis of myofibril pellets remaining after incubation showed a preferential proteolysis of low molecular weight proteins (Fig. 11). However, the 46 kD and 42 kD proteins missing in burnt tuna were not completely hydrolysed during the calpain incubation.

DISCUSSION

On a cellular level, burnt yellowfin tuna was found to be significantly different from unburnt tuna in a

predictable way. The anatomical differences in Z-disc integrity are consistent and quantifiable. Burnt and unburnt tuna are also distinct from one another regarding the amount of 42 and 46 kD protein they contain. Given the unique characteristics of burnt tuna a specific proteolytic pathway is implicated in its formation.

Electron micrographs of white muscle from sport caught yellowfin tuna sampled *post mortem* showed Z-disc damage and *post mortem* edema undistinguishable from that seen in unburnt tissue of partially burnt fish at the Honolulu Fish Auction. Clearly, unburnt tissue from partially burnt fish is not anatomically exceptional, it is simply undergoing changes common to *post mortem* yellowfin tuna

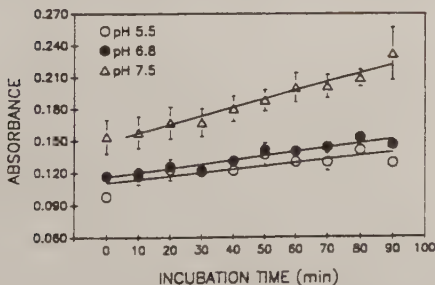


Fig. 10. Quantity of acid-soluble peptides (absorbance measured at 280 nm) released from isolated myofibrils of yellowfin tuna muscle following incubation with calpain. Error bars are SEM. Lines shown are based on linear regression.

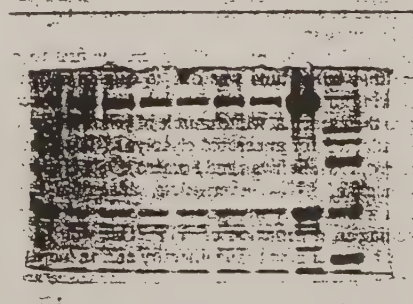


Fig. 11. Polyacrylamide gel of myofibrils incubated with calpain at pH 7.5. Lane 1: actin standard, lanes 2-8: myofibrils incubated for 90, 80, 70, 50, 30, 10 and 0 min, lane 9: high molecular weight standard.

muscle. However, burnt tuna is more than simply accelerated *post mortem* deterioration as suggested by Davie and Sparksman (1986) and Hochachka and Brill (1987). If that were the case we would expect to see all tuna muscle eventually look burnt. However, electron micrographs from muscle sampled 21 days *post mortem* demonstrated that this is not always true.

It was important to establish whether or not burnt tuna was caused by the physical stress of exercise on the myofibrils since all tuna struggle during capture. Myofibrils of captive yellowfin tuna biopsied after strenuous exercise have the same tears mid-A band as occurs in human myofibrils following strenuous sustained exercise (O'Reilly *et al.*, 1987; Warhol *et al.*, 1985), but do not have the frayed Z-discs of burnt tuna. Since cutting in oblique instead of longitudinal section could produce the same impression of mid-A band fractures, we sectioned multiple blocks in multiple orientations and submitted the micrographs for independent evaluation (Evans, pers. comm.) who concurred that we were seeing myofibril tearing. In tuna, exhaustive exercise causes three primary changes in muscle fibers: intracellular edema, a spreading of the myofibrils, with the Z-discs generally intact although often out of register, and tearing of the sarcomere, generally in mid-A-band. In human muscle this is caused by mechanical stress on the myofibril rather than by proteolysis. While exercised muscle shows interesting ultrastructural changes, it does not resemble the specific Z-disc dissolution of burnt tuna myofibrils.

Electron micrographs show that Z-disc disintegration, coupled with intracellular edema are ultrastructural benchmarks of tissue designated as burnt. Since these characteristics are well accepted results of calpain activity (Reddy *et al.*, 1983; Ishiura, 1981), we conclude that the protease calpain is more active in "burnt" muscle than in normal *post mortem* tissue.

Attempts to identify the 46 and 42 kDa proteins using Western blot were unsuccessful, perhaps due to the incompatibility of mammalian antibodies and fish proteins. However, desmin and vimentin, located at the Z-disc have degradation products in this molecular weight range (Lazarides, 1982) which would be partly degraded in normal tissue and completely degraded at higher calpain activation rates. Incubation of isolated myofibrils in calpain produced the expected increase in proteolysis at physiological pH, but failed to show a selective hydrolysis of the 42 and 46 kDa proteins.

Hochachka and Brill (1987) were the first to propose that burnt tuna was due to calpain activation following an increase in intracellular calcium. According to their schema, white muscle of yellowfin tuna are well adapted for anaerobic glycolysis (Castellini and Somero, 1981; Sullivan and Somero, 1980; Guppy and Hochachka, 1978) nevertheless, anaerobic metabolism will cease some minutes or hours after death, resulting in a depletion of ATP. This will, in turn, cause a loss of membrane integrity and an increase in intracellular calcium from extracellular space as well as from SR. High intracellular Ca^{2+} concentrations will activate calpain and the result should be burnt tuna. Yet under the worst of circumstances, only about 25% of handline caught tuna are burnt. Watson *et al.* (1988) proposed that high levels of circulating

catecholamine could account for this difference. Besides their role in cell calcium regulation, catecholamines are also accelerators of calpain proteolysis (Toyo-oka, 1982). While this remains an interesting possibility, the transient nature of catecholamines make it untestable in auction sampled animals. However, there are other conditions which would allow escape from what appears to be an inevitable proteolytic cascade.

Our current hypothesis is as follows. If yellowfin tuna engage in an aerobic capture struggle by using red muscle or are in a poor nutritional state, i.e. have limited intracellular glycogen, they will have little opportunity to accumulate lactate and the accompanying protons before landing. If intracellular pH remains high *post mortem*, and within the range where calpain is most active, proteolysis of intermediate molecular weight proteins is probable. This is consistent with Yu and Lee (1986) and Zeece *et al.* (1986) who found that *post mortem* substrate proteolysis was pH dependent, with muscle incubated at high pH having a specific removal of the Z-disc. Muscle incubated at low pH had well preserved Z-discs but degraded myosin and M-lines, whereas intermediate pH (5.8–6.3) resulted in little proteolysis of any substrate. In other words, yellowfin tuna that become burnt have limited intracellular glycogen which allows a minimal drop of pH and optimal conditions for calpain activity while at the same time inhibiting lysosomal proteases.

Some field evidence indirectly support this hypothesis. More female yellowfin tuna caught near the Hawaiian Islands become burnt during spawning season, when the high metabolic cost of gonadal tissue synthesis could lead to depletion of intracellular glycogen stores (Nakamura, 1987). Although muscle glycogen content of large yellowfin tuna caught near the Hawaiian Islands has never been measured, skipjack tuna (*Katsuwonus pelamis*) caught in the same area appear to be malnourished. High concentrations of muscle anserine and carnosine are indicative of starving skipjack tuna, and higher anserine levels have been found in skipjack tuna caught near the Hawaiian Islands than in fish caught elsewhere (Abe *et al.*, 1985, 1986). Moreover, anserine and carnosine have recently been found to act directly as potentiators of calpain activity (Johnson, 1990). Now that "burnt" tissue can be identified in small quantities of muscle, these possible mechanisms can be investigated.

In conclusion, we have demonstrated that burnt tuna is anatomically and biochemically different from unburnt tuna in a specific and quantifiable way. The degradation of Z-discs and the loss of the 42 and 46 kDa proteins is not caused by exercise alone, nor is it an accelerated generalized *post mortem* proteolysis. While the unique proteolytic pathway leading to burnt tuna bears many of the earmarks of calpain activation, we were unable to establish by incubation that calpain is responsible. It is possible that the same pre-death conditions which increase calpain activity also stimulate another cytoplasmic proteinase which operates independently or synergistically with calpain. Details of the exact proteolytic sequence still need to be described and could provide valuable insights into proteolytic regulation during ischemia.

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DISTRIBUTION OF LARVAL PACIFIC SARDINE, *SARDINOPS SAGAX*, IN SHALLOW COASTAL WATERS BETWEEN OCEANSIDE AND SAN ONOFRE, CALIFORNIA: 1978-1986

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ABSTRACT

Spatial and temporal distributions of larval Pacific sardine, *Sardinops sagax*, were investigated at two nearshore sites between San Onofre and Oceanside, California. Neuston, midwater, and epibenthic samples were collected at night with plankton nets towed at a randomly selected isobath within each of five sampling blocks between the 6-m and 75-m isobaths at each site. The San Onofre site was sampled from January 1978 through September 1986; the site near Oceanside was sampled from July 1979 through September 1986. Sampling frequency varied from weekly to quarterly, depending on other requirements of the study.

The average cross-shelf distribution of larvae differed little from year to year: abundance usually was highest between the 12-m and 45-m isobaths, particularly for yolk-sac and preflexion larvae. Densities were typically highest in midwater. Vertical and cross-shelf distributions were similar at both study sites.

Larvae were found nearly year-round, but were most abundant in summer and fall. Seasonal abundance patterns differed relatively little between sites or from year to year. Abundance was quite low from 1978 to 1980, then increased dramatically to a peak in 1984.

The results of this study, together with other published reports, suggest that the resurgence of the Pacific sardine off southern California in the early 1980s began in 1981 in shallow waters along the central southern California coast.

RESUMEN

Se investigó la distribución espacio-temporal de las larvas de *Sardinops sagax*, la sardina del Pacífico, en dos estaciones costeras entre San Onofre y Oceanside, California. Se colectaron muestras durante la noche en el neuston, a media agua y en el epi-bentos; en cada localidad se hicieron arrastres en curvas isobatas elegidos aleatoriamente en cada uno de cinco bloques de muestreo (entre las curvas iso-

batas de 6 y 75 m). El sitio en San Onofre fué muestreado de Enero de 1978 a Septiembre de 1986, y el cercano a Oceanside de Julio de 1979 a Septiembre de 1986. La frecuencia de muestreo fué variada, de semanal a trimestral, dependiendo de otros requerimientos del estudio.

La distribución promedio de las larvas en sentido perpendicular a la costa varió poco de año a año, encontrándose la máxima abundancia entre las curvas isobatas de 12 y 45 m; esto fué particularmente cierto para los estadios de saco vitelino y pre-flexión. Las densidades más altas se encontraron a media agua. Las distribuciones vertical y en sentido perpendicular a la costa fueron similares en ambos sitios de estudio.

Se encontraron larvas durante todo el año, con máximos en verano y otoño. Los patrones de abundancia estacional difirieron relativamente poco entre los distintos sitios o de año a año. La abundancia larval fué relativamente baja en 1978-80 y subsecuentemente se incrementó de manera substancial hasta alcanzar un máximo en 1984.

Los resultados de este estudio, aunados a otros reportes ya publicados, sugieren que el repunte a principio de los 80 de la sardina del Pacífico en el Sur de California empezó en 1981 en aguas someras de la costa central del Sur de California.

INTRODUCTION

The rise and fall of the Pacific sardine fishery along the west coast of the United States between about 1915 and the mid 1960s has been extensively documented and discussed (e.g., Murphy 1966; Ahlstrom and Radovich 1970; MacCall 1979; Radovich 1982). A minor fishery continued after the mid 1960s until 1974, when a moratorium was declared. In the early 1980s Pacific sardine again began to increase in California waters (e.g., Bedford et al. 1982; Wolf and Smith 1985), and in 1986 a small directed fishery once again was permitted (e.g., Wolf and Smith 1986; Wolf et al. 1987).

Lavenberg et al. (1986), reporting on nearshore ichthyoplankton surveys along the southern California coast, suggested that this resurgence may have begun in shallow coastal waters, as would be

predicted by MacCall's (1983) model of habitat selection by declining fish populations. The purpose of this report is to further document the spatial and temporal distributions of larval Pacific sardine in shallow coastal waters of southern California in the years just before, and during, the resurgence of the early 1980s. This report is based on a longer time series (1978–86) and more complete water-column coverage than have been documented before from the shallow coastal zone.

METHODS

Ichthyoplankton samples were collected from January 1978 through September 1986 along an onshore-offshore transect approximately 1 km south of the San Onofre Nuclear Generating Station (SONGS), and from July 1979 through September 1986 along a similar transect off Stuart Mesa, approximately 17 km south of the SONGS transect (figure 1). The sampling methodology, which was the same at both sites, was described by Barnett et al. (1984), Walker et al. (1987), and Moser and Watson (1990). Briefly, a stratified random design (Snedecor and Cochran 1967) was used to sample the neustonic (top 16 cm), epibenthic (bottom 67 cm), and remaining midwater layers of the water column along a randomly selected isobath within each of five blocks at each site on each survey date. These blocks were defined by bottom depth: (A) 6–9 m, (B) 9–12 m, (C) 12–22 m, (D) 22–45 m, and (E) 45–75 m.

Three different nets, equipped with 0.333-mm-mesh Nitex and flowmeters, were used to sample the entire water column. A Manta net, 88 cm wide

by 16 cm deep, was used to sample the neuston; a 71-cm bongo net was used for a stepped-oblique tow through the midwater column; and an Auriga net (MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627) 2 m wide by 0.5 m high was used in the epibenthic stratum. All tows were taken at night along the chosen isobaths, at about 1 m/s for a fixed time selected to filter a target volume of 400 m³. Samples were not collected in block E on two dates in 1985 because of equipment problems. All samples were preserved in the field in 10% Formalin in seawater.

Although this study yielded information on the temporal and spatial distributions of larval Pacific sardine, acquiring such information was not its specific intent. Instead, the study was designed to predict, and subsequently measure, how two new SONGS units would affect the plankton. Consequently, sampling frequency varied considerably, according to the changing requirements of the power plant study. Sampling frequency ranged from approximately weekly toward the end of the predictive phase of the study (1980) to quarterly during the 3-year interim between the plant's preoperational and operational phases (1981–83). Most sampling was done in spring and summer (March–September).

In the laboratory, most samples were subsampled with a Folsom plankton splitter before being sorted for fish larvae (average for all samples = 25% sorted, range = 3.1%–100%). After sorting, each subsample was checked to ensure that at least 90% of the larvae were removed. Larval Pacific sardine were counted in four developmental stages (yolk-sac, preflexion, notochord flexion, postflexion) for a subset of the 1978–79 samples (one transect per survey) and for all subsequent samples. A small proportion of the larvae were too damaged to allow unequivocal identification of developmental stage; since most of those were small, all were arbitrarily assigned to the preflexion class. The count data were converted to number per 100 m³, and these density data were used to calculate abundance (number under 10 m² in each block and number in a 1-m-wide strip between the 6–75-m isobaths at each site). No corrections were made for the missing block E values on the two 1985 surveys; for those dates cross-shelf abundance values may be somewhat underestimated.

The density data and abundance-per-block data were transformed by log ($x + 0.1$) and analyzed using ANOVA and Student-Neuman-Keuls (SNK) multiple range tests to examine spatial patterns (results evaluated at $\alpha = 0.05$). The surveys lacking

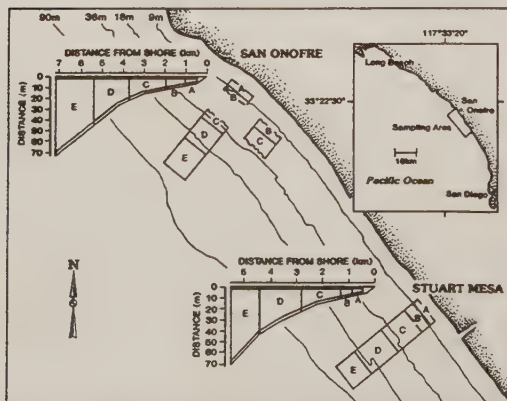


Figure 1. Locations of the study sites along the southern California coast, with schematic profiles of the bathymetry at each site. On each survey date, a sample was taken at a randomly selected isobath within each of the five blocks (A–E) at each site.

block E samples were deleted from the statistical analyses in order to maintain a balanced design, and surveys during which sardine larvae were not collected were deleted because they contained no information about location. Incidence was calculated as the percentage of total tows that contained Pacific sardine larvae.

Seasonal patterns and interannual changes in abundance were examined qualitatively with the cross-shelf abundance values (number/m between the 6–75-m isobaths); these patterns are presented in figures.

RESULTS

Spatial Distribution

Overall, larval Pacific sardine at both study sites were most abundant in block D, between the 22-m and 45-m isobaths; abundance decreased at the shoreward and seaward stations. The most shoreward station (6–9-m depth) had the lowest abundance. Cross-shelf patterns varied somewhat from year to year, but in general they were similar at both sites throughout the study (figure 2).

There was slight evidence of a possible ontogenetic seaward shift in a cross-shelf distribution at both sites, with yolk-sac larvae most abundant in block C, preflexion and flexion larvae most abundant in block D, and postflexion larvae slightly more abundant in block E (figure 3). However, most of these patterns were not statistically detectable (table 1). At San Onofre, only the high abundance of preflexion larvae in block D could be distinguished from their low abundance in block A. At Stuart Mesa, higher abundances of preflexion larvae in blocks C, D, and E were distinguishable from lower abundance in blocks A and B, whereas for flexion larvae the higher abundance in block D was distinguishable from the lower abundance in block A (table 1).

Larvae occurred most frequently in midwater (incidence overall 20% at San Onofre and 28% at Stuart Mesa), secondarily in the neuston (15% at San Onofre, 22% at Stuart Mesa), and least in the epibenthos (8% at San Onofre, 11% at Stuart Mesa). All stages appeared more frequently in midwater than in the other strata. Yolk-sac and preflexion larvae were somewhat less common in the neuston and relatively uncommon in the epibenthos, while flexion and postflexion larvae appeared almost equally frequently in neustonic and epibenthic samples.

Mean larval density values largely reflected the incidence values, and apparently differed little between study sites. Yolk-sac and preflexion larvae

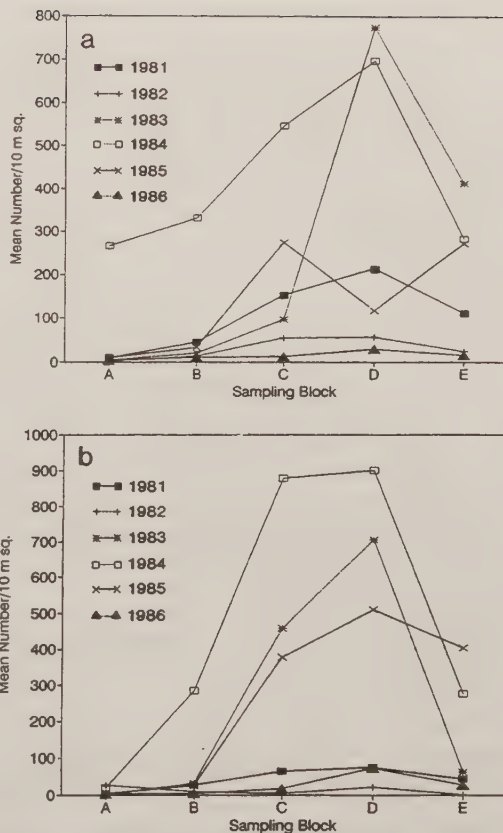


Figure 2. Mean number of larval Pacific sardine under 10 m² of sea surface in each sampling block. The very low abundances in 1978–80 are not shown. All larval stages are pooled. a = San Onofre; b = Stuart Mesa.

typically were most numerous in midwater and neuston samples (figures 4 and 5). Yolk-sac larvae were rare in epibenthic samples, but preflexion larvae were moderately dense in the epibenthic stratum of the more shoreward blocks (figures 4 and 5). Flexion and postflexion larvae were distributed more uniformly through the water column, although somewhat lower near shore and higher farther from shore (figures 4 and 5).

Analysis of variance demonstrated significant differences in density among vertical strata for yolk-sac and preflexion larvae at both sites, but failed to indicate significant differences among strata for the older larvae at San Onofre (table 2). There were no statistically significant differences between blocks (block main effects) at San Onofre, and only one significant block X stratum interaction at either site

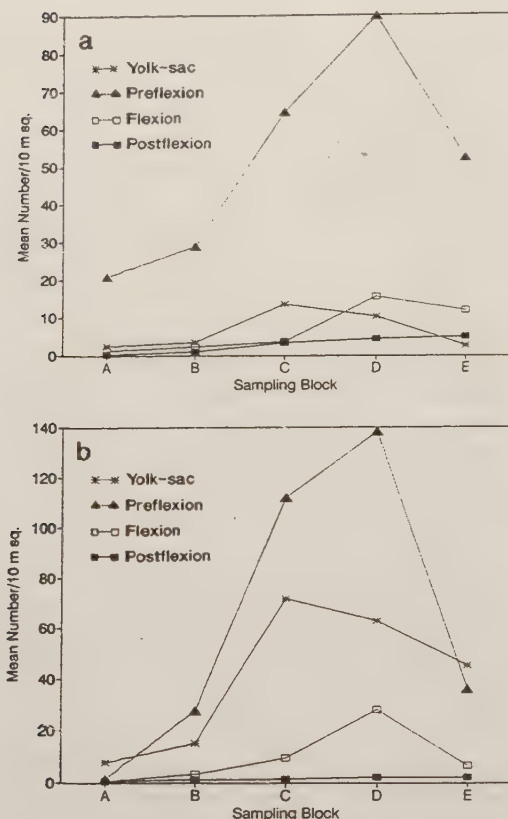


Figure 3. Mean number of larval Pacific sardine under 10 m² of sea surface in each sampling block. Each developmental stage is plotted separately; all years are pooled. a = San Onofre; b = Stuart Mesa.

(postflexion larvae at Stuart Mesa), although some block main effects and interactions approached significance ($0.10 > p > 0.05$; table 2).

Temporal Distribution

Seasonal pattern. Larval sardines were collected in every month except January and February, with a distinct maximum in summer and fall (figure 6). Incidence (percent positive collections, all years at both sites pooled) increased from 7%–27% between March and May to 60%–79% during June–September, then declined to the winter nadir, except during December, when six of seven transects yielded sardines. Although incidence varied somewhat from year to year and increased substantially beginning in 1981, there were no consistent changes to suggest a shift in the seasonal pattern over the nine years of the study (figure 7). Incidence at the

TABLE 1
 Results of ANOVA and SNK Analyses on Cross-Shelf Distributions of Larval Pacific Sardine

Stage	N	ANOVA result		SNK result				
		F	P					
San Onofre								
Yolk-sac	17	0.67	>.05	<u>E</u>	<u>A</u>	<u>B</u>	<u>D</u>	<u>C</u>
Preflexion	32	2.44	<.05	<u>A</u>	<u>E</u>	<u>B</u>	<u>C</u>	<u>D</u>
Flexion	21	1.83	>.05	<u>A</u>	<u>B</u>	<u>D</u>	<u>C</u>	<u>E</u>
Postflexion	22	0.61	>.05	<u>A</u>	<u>B</u>	<u>D</u>	<u>E</u>	<u>C</u>
Stuart Mesa								
Yolk-sac	21	1.96	>.05	<u>E</u>	<u>A</u>	<u>B</u>	<u>D</u>	<u>C</u>
Preflexion	30	8.19	<.05	<u>A</u>	<u>B</u>	<u>C</u>	<u>E</u>	<u>D</u>
Flexion	22	2.25	>.05; <.10	<u>A</u>	<u>B</u>	<u>E</u>	<u>C</u>	<u>D</u>
Postflexion	19	0.49	>.05	<u>E</u>	<u>C</u>	<u>D</u>	<u>B</u>	<u>A</u>

Only positive survey dates (N) were included in the analyses. SNK results are shown with sampling blocks (A–E) ordered from lowest geometric mean abundance (left) to highest geometric mean abundance (right). Sampling blocks joined by underlines are statistically indistinguishable (evaluated at $\alpha = 0.05$).

Stuart Mesa site tended to be a little lower than at San Onofre in spring (typically 50%–90% of San Onofre values), but a little higher in summer (usually 110%–140% of San Onofre values).

Abundance largely mirrored incidence, with none to few larvae in winter and spring, rapidly increasing abundance to a maximum in September and October, then a rapid decline to the winter nadir (figure 6b). Apart from a substantial increase in abundance that began in 1981, there were no consistent year-to-year changes that would suggest a shift in seasonal pattern (appendix). Patterns were similar at both study sites, except that the summer-fall peak was smaller and earlier at San Onofre than at Stuart Mesa (figure 6b). The high larval incidence in December surveys noted above was attributable to consistent collection of small numbers of larvae.

Incidence and abundance of yolk-sac larvae were examined in order to better estimate the spawning season. Almost all yolk-sac larvae were collected between May and October (one transect occupancy each in March 1980 and December 1983 also yielded yolk-sac larvae). Incidence increased steadily from 16% in May to 50% in August, then declined steadily to the winter minimum, indicating that spawning takes place principally in summer (figure 8a). There were no consistent differences in seasonal incidence over the years to suggest a shift in spawning season. Incidence was higher at Stuart Mesa than at San Onofre (typically 130%–200% of San Onofre values) in summer and fall.

Abundance of yolk-sac larvae differed somewhat from incidence (figure 8). Abundance did generally

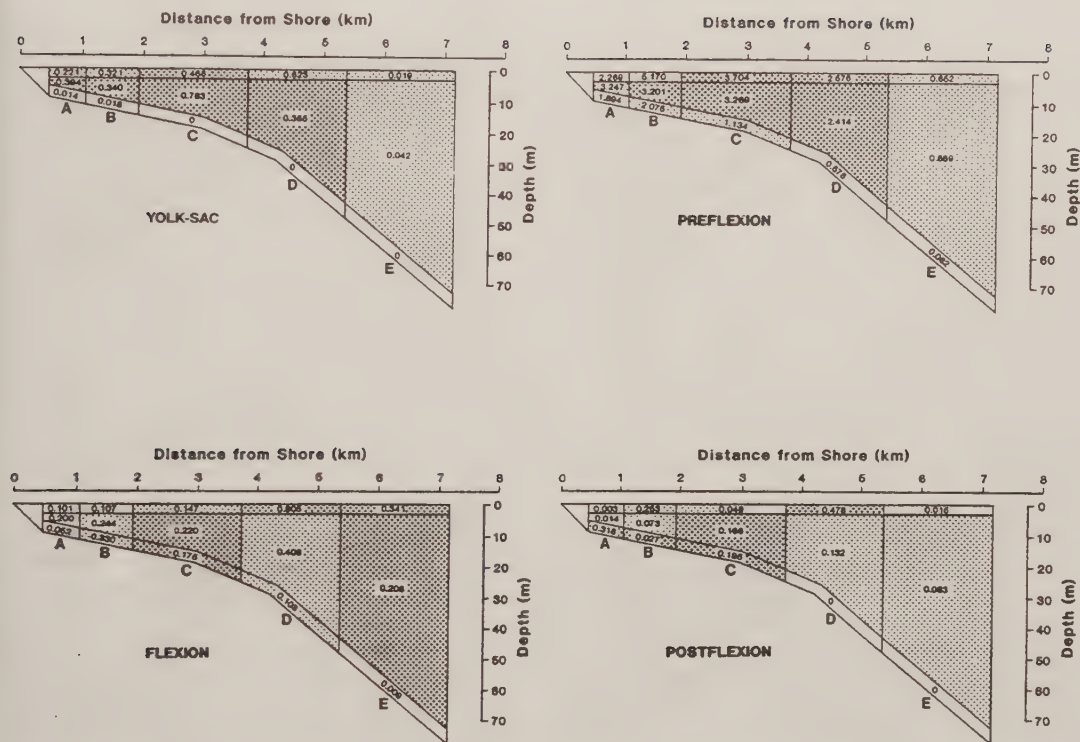


Figure 4. Mean number of larval Pacific sardine per 100 m³ of water in each stratum (neuston, midwater, epibenthos) in each sampling block at San Onofre. Each developmental stage is plotted separately; all years are pooled. Neustonic and epibenthic strata are vertically exaggerated in these schematic representations. Shading indicates rankings of the geometric mean densities from the ANOVA on density: dark = the five highest-ranked means; light = the five middle-ranked means; white = the five lowest-ranked means.

increase from spring to a fall maximum, but with two or three smaller peaks at about 2-month intervals during the spring and summer. The minor peaks were about one month earlier at San Onofre than at Stuart Mesa, but the major peak was in October at both sites (figure 8b). The abundance of yolk-sac larvae varied considerably from year to year, but there were no consistent changes to suggest a shift in spawning season.

Interannual change. Larval Pacific sardine were collected in relatively few of the 1978–80 samples (figures 7, 9, 10): incidence in those years ranged from a low of 2% in 1979 to 6% in 1980. Incidence increased dramatically in 1981 (to 39%), reached a maximum of 44% in 1984, and remained above 20% through 1986.

Larval abundance likewise was quite low in 1978–80, especially in 1979, then increased substantially,

peaking in 1984 (figures 9a, 10a; appendix). The initial increase was somewhat larger at San Onofre, but subsequently tended to be higher at the Stuart Mesa site.

These initial increases of larval Pacific sardine in 1981 were largely attributable to preflexion and older stages. The incidence of yolk-sac larvae did not begin to increase until 1982 (figures 9a, 10a); yolk-sac abundance did not increase markedly until 1984 (figures 9b, 10b). Yolk-sac larval incidence peaked near 20% at both sites in 1984, then by 1986 returned to the low levels (<5%) typical of the early years of the study. Yolk-sac larval abundance also peaked at San Onofre in 1984, but at Stuart Mesa it continued to increase to a much higher peak in 1985. At both sites, 1986 abundances were quite low, comparable to the levels characteristic of the first years of the study.

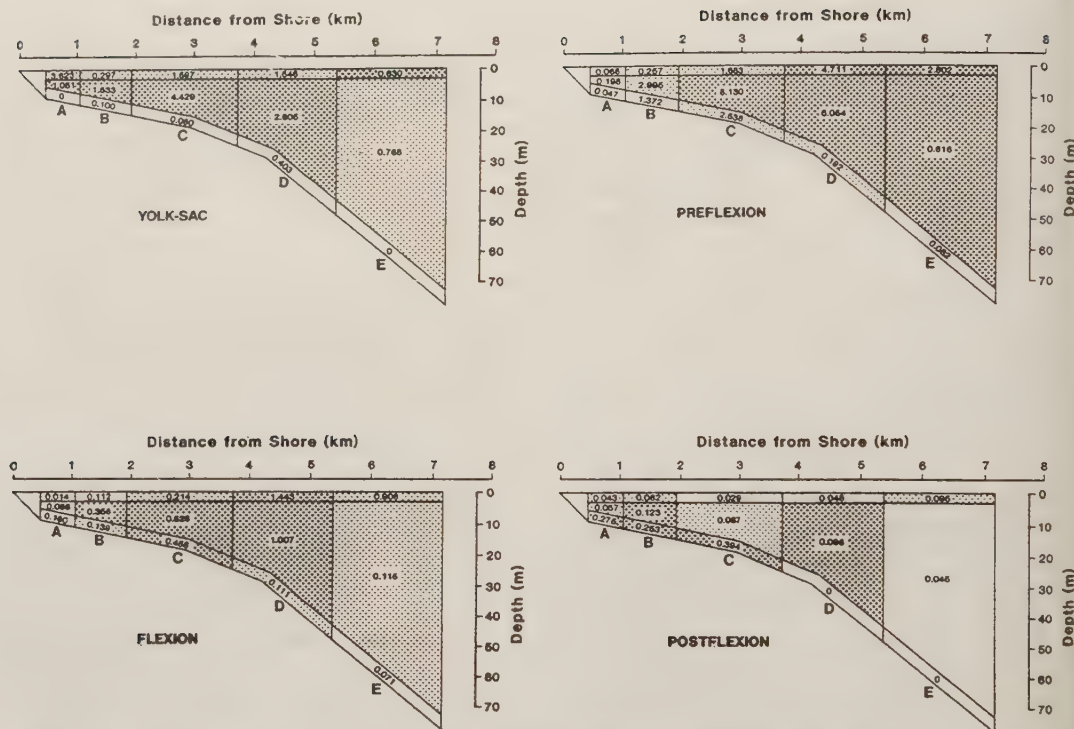


Figure 5. Mean number of larval Pacific sardine per 100 m³ of water in each stratum (neustonic, midwater, epibenthos) in each sampling block at Stuart Mesa. Each developmental stage is plotted separately; all years are pooled. Neustonic and epibenthic strata are vertically exaggerated in these schematic representations. Shading indicates rankings of the geometric mean densities from the ANOVA on density: dark = the five highest-ranked means; light = the five middle-ranked means; white = the five lowest-ranked means.

DISCUSSION

Spatial Distribution

Lavenberg et al. (1986, 1987) showed that over the southern California continental shelf, Pacific sardine eggs were more abundant shoreward from the 36-m isobath than at the 75-m isobath during 1978–86, suggesting that the shallow coastal zone was an important spawning area in those years. In both the Lavenberg et al. 1986 study and this one, Pacific sardine larvae were most abundant in this same zone. This was particularly true for younger larvae in this study: yolk-sac and preflexion larvae were usually most abundant in samples collected between the 12-m and 45-m isobaths, and least abundant in samples collected shoreward and seaward of those depths.

Cross-shelf patterns were much less consistent for the older larvae, suggesting that they were more patchily distributed and that the patches were more

widely dispersed across the inner half of the continental shelf. There was no evidence that larvae attempted to remain in the shallow zone, and only a slight suggestion that the older larvae made any directed movement away from it. CalCOFI ichthyoplankton surveys in 1978, 1981, and 1984 yielded few larval Pacific sardines along the transect lines (80–97) off southern California (Ambrose et al. 1988; Sandknop et al. 1988; Stevens et al. 1990), except in March, June, and July 1984, when a few relatively large catches were made, mainly at nearshore stations (Stevens et al. 1990). Together, these studies suggest that between 1978 and 1984–86 sardines spawned chiefly in the zone bounded by the 12-m and 45-m isobaths, and that larvae slowly dispersed from this spawning center, but remained primarily over the continental shelf.

Phytoplankton and microzooplankton biomass usually display onshore-offshore gradients along the southern California coast, with higher values nearer

TABLE 2
Summary of ANOVA on Density (Number per 100 m³) in
the 15 Strata (3 Vertical Strata × 5 Cross-Shelf Blocks)
Sampled at Each Location

Larval stage	Source	d.f.	M.S.	F	P
San Onofre					
	Yolk-sac				
	Blocks	4	0.66	1.72	>0.10
	Strata	2	6.01	15.77	<0.01
	Interaction	8	0.25	0.67	>0.10
Preflexion	Error	225	0.38		
	Blocks	4	1.32	2.26	>0.05; <0.10
	Strata	2	4.68	8.02	<0.01
	Interaction	8	0.33	0.56	>0.10
	Error	480	0.58		
Flexion	Blocks	4	0.85	2.31	>0.05; <0.10
	Strata	2	0.72	1.95	>0.10
	Interaction	8	0.39	1.06	>0.10
	Error	300	0.37		
	Blocks	4	0.43	1.97	>0.05; <0.10
Postflexion	Strata	2	0.14	0.64	>0.10
	Interaction	8	0.37	1.72	>0.05; <0.10
	Error	315	0.22		
Stuart Mesa					
	Yolk-sac				
	Blocks	4	0.88	1.79	>0.10
	Strata	2	7.67	15.56	<0.01
	Interaction	8	0.56	1.13	>0.10
Preflexion	Error	300	0.49		
	Blocks	4	4.63	8.73	<0.01
	Strata	2	7.81	14.73	<0.01
	Interaction	8	0.70	1.33	>0.10
	Error	435	0.53		
Flexion	Blocks	4	2.24	5.86	<0.01
	Strata	2	0.30	0.78	>0.10
	Interaction	8	0.48	1.26	>0.10
	Error	315	0.38		
	Blocks	4	0.53	2.47	<0.05
Postflexion	Strata	2	0.25	1.16	>0.10
	Interaction	8	0.44	2.03	<0.05
	Error	270	0.22		

Only positive dates were included in the analyses.

shore (e.g., Mullin 1986). The high rates of phytoplankton production, and the high concentrations of microzooplankton and macrozooplankton near shore (e.g., Beers and Stewart 1967; Lasker 1978; Petersen et al. 1986; Barnett and Jahn 1987) should provide a good feeding environment for Pacific sardine, and might have enhanced egg quality or production as well as larval survival during the study period. MacCall (1983, 1990) predicted that just such a productive nearshore zone would support the remnants of a depleted population such as the Pacific sardine, and that any subsequent resurgence of the population would originate from this core area. This may partially explain the observed increase.

In the shallow nearshore zone there was little evidence of strong vertical stratification, except that the younger larvae (yolk-sac and, to a lesser extent, preflexion) were rare in the lower 0.5 m of the water column. (These samples, however, were all collected at night, and the vertical distributions observed may not reflect daytime patterns; e.g., Silliman 1943).

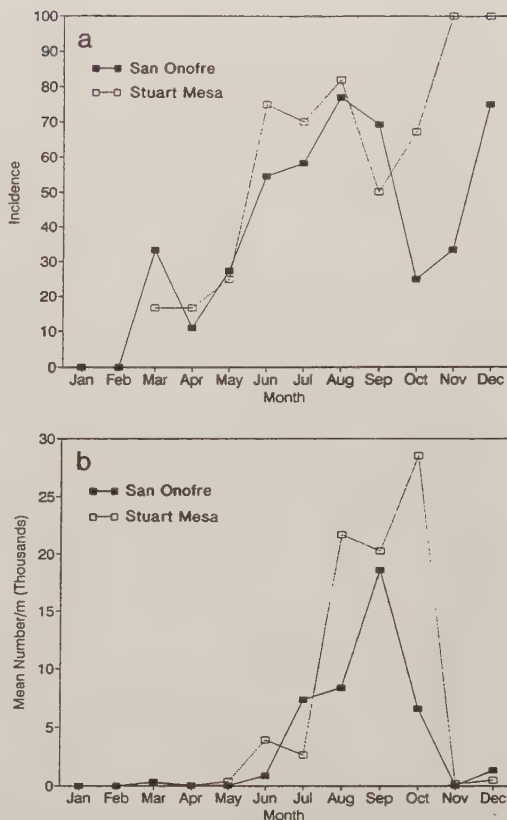


Figure 6. a, Monthly mean incidence (percent positive collections) and b, abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) of larval Pacific sardine. All developmental stages and all years are pooled.

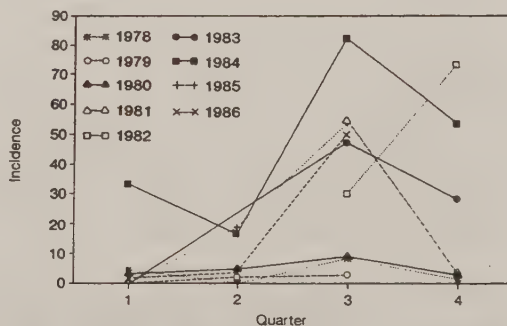


Figure 7. Incidence (percent positive collections) of larval Pacific sardine, 1978-86, plotted by quarter. All developmental stages, and data from both study sites are pooled.

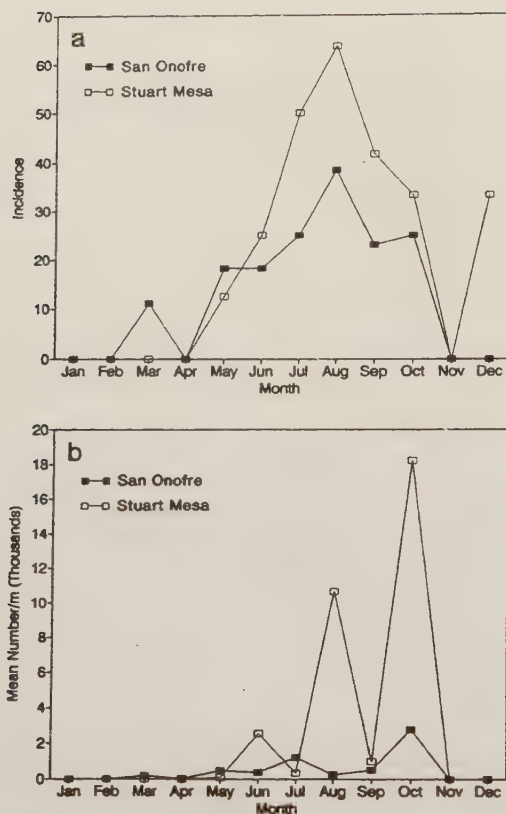


Figure 8. a, Monthly mean incidence (percent positive collections) and b, abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) of yolk-sac larval Pacific sardine. All years are pooled.

Postflexion larvae, on the other hand, tended to appear in the lower 0.5 m, but usually only at shallower depths (≤ 22 m). By avoiding the epibenthic stratum, the small larvae may avoid being eaten by the many large larval and small juvenile fishes resident on the shallow shelf (e.g., croakers, gobies: Barnett et al. 1984; Brewer and Kleppel 1986; Jahn and Lavenberg 1986). The postflexion larvae may be large enough to avoid this danger. But whether predator avoidance does actually limit the vertical distribution of larval Pacific sardine in nearshore waters is purely speculative at this point.

Temporal Distribution

Ahlstrom (1960, 1967) showed that off southern California in the 1950s, Pacific sardines spawned largely in spring and summer, and occasionally at other seasons during warmer years. From 1978 to

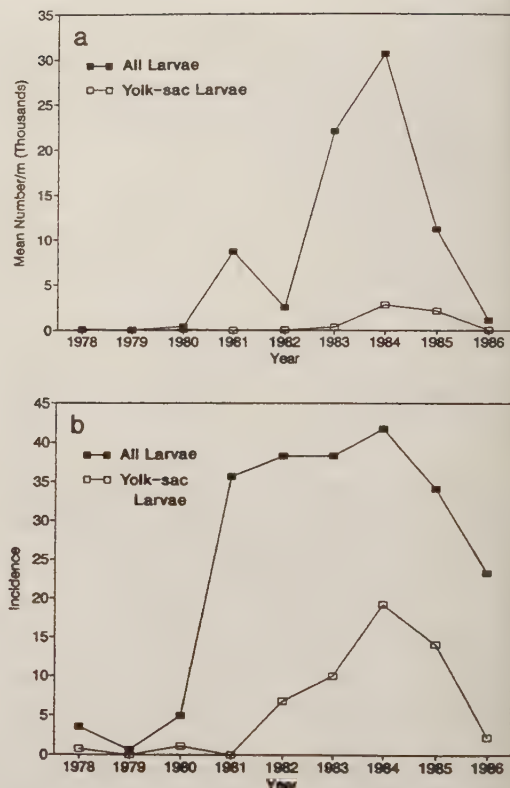


Figure 9. a, Annual mean abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) and b, incidence (percent positive collections) of larval Pacific sardine off San Onofre.

1986, spawning was nearly year-round, but was almost always highest in summer or fall (Brewer and Smith 1982; Lavenberg et al. 1986, 1987; this study). It has been speculated that this shift in the principal spawning season represented a movement into southern California waters of a later-spawning southern stock (Brewer and Smith 1982; Lavenberg et al. 1986), perhaps facilitated by the somewhat warmer temperature regime during those years.¹ An alternative suggestion that the warmer temperature may have allowed more extended spawning by the local population (e.g., Lavenberg et al. 1986), as happened in the late 1950s (Ahlstrom 1960), seems

¹S. Hernández-Vázquez, D. Lluch-Belda, D. Lluch-Cota, and C. Salinas-Zavala. Interannual variability of sardine and anchovy eggs and larvae in the Southern California Bight related to sea surface temperature, upwelling index and small zooplankton biomass: 1951–1988. Calif. Coop. Oceanic Fish. Invest. Ann. Conf. 22–24 October 1991, Lake Arrowhead, Calif.

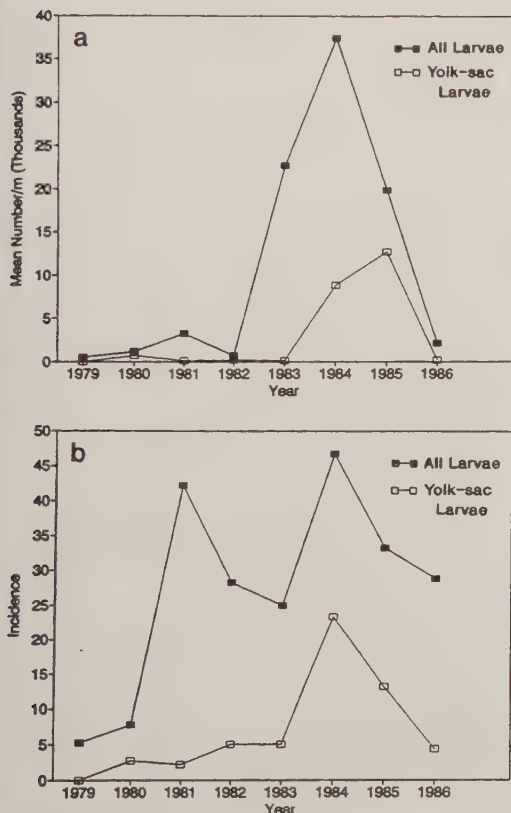


Figure 10. a, Annual mean abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) and b, incidence (percent positive collections) of larval Pacific sardine off Stuart Mesa.

unlikely to solely account for the strong summer-fall spawning peak, but it may well have contributed to both the extended spawning season and the shift in timing. Lavenberg et al. (1987) noted a return to spring-summer spawning in 1986; no such shift was apparent in this study.

The resurgence of the Pacific sardine began in the early 1980s (Wolf and Smith 1985; Lavenberg et al. 1986, 1987); I suggest that it started in 1981. The initial increase near San Onofre apparently was not attributable to local spawning, since increases for yolk-sac larvae lagged total larvae by a considerable period. Lavenberg et al. (1986) reported that sardine larval abundance first increased north of San Onofre, primarily in the Seal Beach area in 1982, and subsequently spread north and south along the coast

in 1983. Because nearshore currents along the southern California coast usually flow alongshore toward the south (Winant and Bratkovich 1981), it seems reasonable to speculate that the early increases in larval abundance in the San Onofre vicinity represented southward alongshore advection of larvae from some spawning site farther north (but probably not as far north as Seal Beach, since an egg spawned there would be a well-developed larva or juvenile 2 to 5 weeks old by the time it reached San Onofre). Alternatively, yolk-sac larvae may simply have not been collected, or not retained in the nets if they were collected, during the early years of this study. Although it seems likely that yolk-sac sardine larvae were not quantitatively sampled by the 0.333-mm-mesh nets used (because of extrusion), no systematic change during the course of the study would have caused the yolk-sac larvae to be undersampled more in some years than in others. The precipitous decline in larval abundance in 1986 is consistent with the report by Lavenberg et al. (1987) that no Pacific sardine eggs were collected off San Onofre in 1986 (although they were abundant at the Santa Monica Bay and San Pedro Bay sites).

In summary, on the basis of this and other studies, it appears that the resurgence of the Pacific sardine off southern California began in 1981 in shallow waters off the central coast.

ACKNOWLEDGMENTS

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I thank the many technicians at MEC Analytical Systems, Inc. who spent long hours collecting and processing the samples that provided the basis for this study. I thank H. G. Moser for reviewing an earlier draft of the manuscript, and D. Foster for typing it.

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APPENDIX

Number of Larval Pacific Sardine under a 1-m-Wide Strip between the 6-m and 75-m Isobaths off San Onofre and Stuart Mesa on Each Survey Date: 1978-86

Starting date	Number of larvae (thousands)		Starting date	Number of larvae (thousands)	
	San Onofre	Stuart Mesa*		San Onofre	Stuart Mesa*
1978			1980, cont'd.		
24 Jan.	0		4 Aug.	4.156	4.482
16 Feb.	0		11 Aug.	0.793	0
6 Mar.	0.231		18 Aug.	1.367	3.256
21 Mar.	0		25 Aug.	0.059	1.103
3 Apr.	0		1 Sept.	0	0.320
26 Apr.	0		8 Sept.	0.022	0
8 May	0		22 Sept.	0.002	0
22 May	0		26 Sept.	0	0
5 June	0		29 Sept.	0.002	0
21 June	0		6 Oct.	0	0
7 July	0.355		13 Oct.	0	0.003
17 July	0.002		1981		
2 Aug.	0.002		7 July	24.831	9.080
16 Aug.	0		15 Sept.	1.194	0.432
7 Sept.	0.851		17 Nov.	0	0.185
3 Oct.	0		1982		
8 Nov.	0.001		9 Mar.	0	0
28 Nov.	0		13 July	5.127	1.965
27 Dec.	0		26 Aug.	0.099	0.373
1979			10 Dec.	4.677	0.314
3 Feb.	0		1983		
26 Feb.	0		12 May	0	0
26 Mar.	0		19 July	1.018	0.954
25 Apr.	0		23 Aug.	86.468	89.389
23 May	0.002		14 Dec.	0.423	0.587
25 June	0		1984		
24 July	0	0	13 Mar.	0.886	1.411
22 Aug.	0	2.527	7 May	0	0
23 Aug.	0	0	30 May	6.104	2.805
20 Sept.	0	0	19 June	0.903	0.987
21 Sept.	0	0	23 Aug.	13.770	11.067
1980			13 Sept.	196.829	197.311
10 Mar.	1.783	0	4 Oct.	26.251	85.524
17 Mar.	0	0	21 Dec.	0.025	0.473
24 Mar.	0	0	1985		
4 Apr.	0	0	21 Jan.	0	0
14 Apr.	0	0	22 Apr.	0	0
23 Apr.	0	0	13 May	0.056	0.051
5 May	0	0	4 June	4.624	7.667
12 May	0	0	25 June	0.920	0.001
19 May	0	0	18 July	54.868	3.971
26 May	0	0	6 Aug.	0.028	0.327
2 June	1.389	1.384	26 Aug.	2.108	126.126
9 June	0	0	12 Sept.	38.030	40.550
17 June	1.350	0	1986		
24 June	0	0	5 Mar.	0	0
30 June	0.002	21.332	1 Apr.	0	0.001
7 July	0	2.421	30 Apr.	0.055	0
14 July	0	0	21 July	1.687	7.748
21 July	0	0.001	2 Sept.	4.283	4.355
28 July	0	0	25 Sept.	0.518	0.516

*Sampling began at the Stuart Mesa site in July 1979.

LARVAL DEVELOPMENT OF SARGO
(*ANISOTREMUS DAVIDSONII*) AND SALEMA
(*XENISTIUS CALIFORNIENSIS*) (PISCES: HAEMULIDAE)
FROM THE SOUTHERN CALIFORNIA BIGHT

William Watson and H. J. Walker, Jr.

ABSTRACT

Size series of 116 *Anisotremus davidsonii* (2.2–24.9 mm) and 131 *Xenistius californiensis* (2.2–41.7 mm) from field collections were examined for pigmentation, and most specimens were measured to determine morphometric characteristics. Subsets of 39 *A. davidsonii* (2.9–23.6 mm) and 25 *X. californiensis* (2.7–24.1 mm) were cleared and stained to examine skeletal development. Pigment in both species is largely limited to the ventrum and to the dorsal surface of the gut and swimbladder throughout larval development. Both species subsequently develop rather heavy dorsal and dorsolateral pigment; small juveniles display the longitudinal stripes that are well known in juvenile Haemulinae. Both species are moderately slender, with preanal length roughly half of body length. Development in both is gradual, with no marked changes in proportions. Both look like typical haemulines. Skeletal development differs little from that described for other haemulines. Bones of the jaws, operculum, and suspensorium are among the first to ossify, usually before notochord flexion. Ossification of neural and haemal arches and spines and vertebral centra, except the urostyle, is anterior to posterior. Pterygiophores and soft rays form first in the middle of the dorsal and anal fins in both species; addition is both anterior and posterior. Addition of dorsal spines begins posteriorly, but then may continue from anterior to posterior. Larval sargo and salema are distinguished from similar larvae off California and northern Baja California primarily by a combination of myomere count and ventral pigment on the tail. Larval sargo typically have pigment on the peritoneum just anterior to the liver, while larval salema do not. Larval salema usually have a melanophore under the anterior hindbrain, while preflexion stage larval sargo usually do not. After notochord flexion sargo are deeper-bodied than salema. Dorsal fin ray counts allow easy separation of postflexion and older sargo (14–15) from salema (12–13).

In California waters the percoid family Haemulidae is represented by two species: *Anisotremus davidsonii*, the sargo, and *Xenistius californiensis*, the salema. Sargo ranges from the Gulf of California to Santa Cruz Island off southern California, while salema ranges from Peru to Monterey, California (Feder et al., 1974; Miller and Lea, 1972). Sargo was successfully introduced to the Salton Sea in 1951 (Walker et al., 1961). Both species are common in the nearshore Southern California Bight, where the sargo is a highly regarded sport fish. The smaller salema is of minor value as a sport species. The larvae of both species occur during summer in the Southern California Bight where they are essentially restricted to the shallow continental shelf (Ambrose et al., 1988; Sandknop et al., 1988; Stevens et al., 1990; Walker et al., 1987). Feder et al. (1974) noted that juveniles appear close to shore in late summer, in depths of 2–5 m.

Published accounts of larval development are lacking for both species although a postflexion salema was illustrated by Johnson (1984). The species were not distinguished from one another prior to this study (originally presented, in part, at the 1982 California Cooperative Oceanic Fisheries Investigations annual conference, Idyllwild, California, October 1982): both typically were identified as sargo.

In this paper we describe the larval development of sargo and salema, including skeletal development, to facilitate identification of these species in ichthyoplank-

ton samples and as a potential aid in studies of percoid systematics (Johnson, 1984).

MATERIALS AND METHODS

Larvae, collected near San Onofre, California (ca. 75 km northwest of San Diego) (Barnett et al., 1984), were sorted from 5–10% seawater-Formalin fixed plankton samples, and transferred to sodium-borate buffered 2.5% seawater-Formalin. Juveniles were collected by dipnet near San Diego, California, fixed in Formalin, and stored in 50% isopropanol. The juveniles and all illustrated specimens are stored in the Scripps Institution of Oceanography Marine Vertebrates Collection (SIO); all others are stored at the National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla Laboratory.

Specimens were examined under a binocular dissecting microscope equipped with an ocular micrometer. Counts and measurements (to the nearest 0.1 mm) were made on the left side. The following dimensions were recorded for each specimen: standard length, total length, pre-anus length, body depth at pectoral fin insertion, eye diameter, snout length, pre-dorsal fin length, pre-anal fin length, and length of longest preopercular spine (dimensions defined by Potthoff et al., 1984; Saksena and Richards, 1975; Stevens and Moser, 1982). Larval lengths refer to standard length unless otherwise specified. Drawings were made with the aid of a camera lucida.

Descriptions are based on the larvae of 111 sargo and 124 salema, and on 5 sargo and 7 salema juveniles. Representative series of 39 sargo and 25 salema were cleared and stained with alcian blue and alizarin red-S, following the method described by Potthoff (1984).

DESCRIPTION OF LARVAE

Anisotremus davidsonii

Pigmentation (Figs. 1–4).—Pigmentation of sargo is largely restricted to the isthmus, gut and swimbladder, and ventral margin of the tail through most of larval development. During the preflexion stage 10–23 melanophores (mode = 16–17), usually of uniform size, are evenly-spaced along the ventral margin of the tail, beginning at the first or second postanal myomere (a melanophore just above the hindgut, at the last pre-anal myomere, is present in 30% of preflexion specimens <4.5 mm, but is absent thereafter). The number of ventral tail melanophores decreases during notochord flexion to 10–17 (mode = 14) but subsequently changes little (mode = 13–14 during postflexion, 12 during the early juvenile stage). The ventral tail melanophores begin to extend internally during the late preflexion stage; the first 1–4 (usually 1 or 2) become entirely internal and disappear soon after the beginning of notochord flexion. As the anal fin develops (beginning at ca. 4.4 mm), 4 to 7 melanophores move ventrad onto the anal ray bases. The last melanophore along the anal fin base frequently is embedded above the last ray in larvae and the more posterior melanophores also become embedded in juveniles. The anal fin is unpigmented except for the melanophores along the ray bases.

During the preflexion stage 0–5 (mode = 1) small melanophores occur ventrally along the posterior end of the notochord. These melanophores become situated at the bases of developing principal caudal fin rays, usually at one or more of the lower five rays. In late larvae, additional caudal fin melanophores develop along some of the lower principal rays (ca. 12.6 mm), and during the early juvenile stage melanophores develop along some of the upper principal rays (ca. 17 mm). Between 17.2 and 24.9 mm a stripe along the lateral midline of the body extends onto the caudal fin.

Little external pigment develops on the dorsal or lateral surfaces of the trunk or tail, except over the gut area in larvae larger than ca. 8 mm. Near the end of the larval stage (ca. 12.6 mm) a few small melanophores appear along the dorsal margin just anterior to the dorsal fin (Fig. 3b). During the early juvenile stage

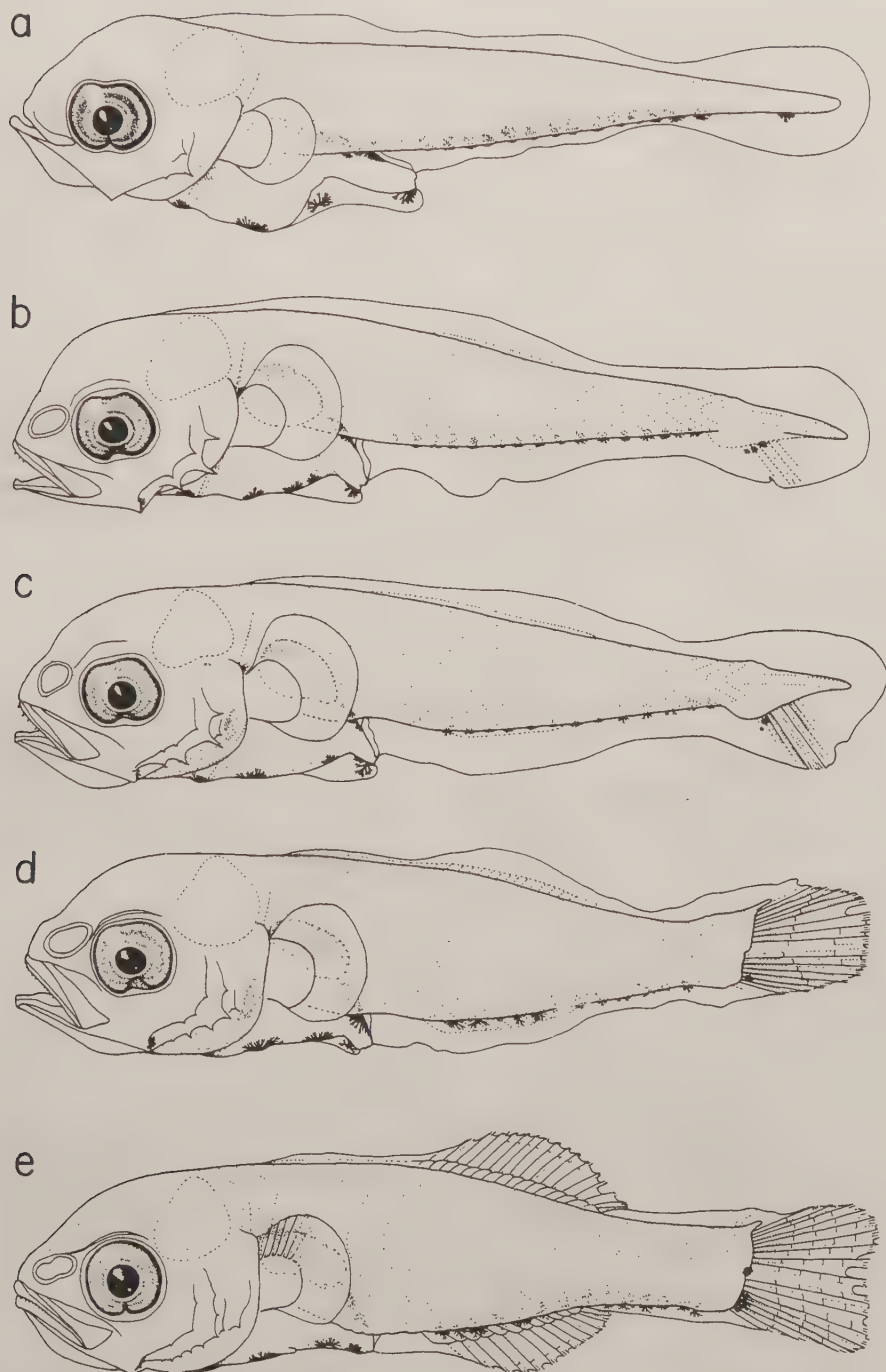


Figure 1. Larval sargo, *Anisotremus davidsonii* (all SIO 91-135): a. 3.0 mm; b. 4.1 mm; c. 4.9 mm; d. 5.2 mm; e. 7.2 mm.

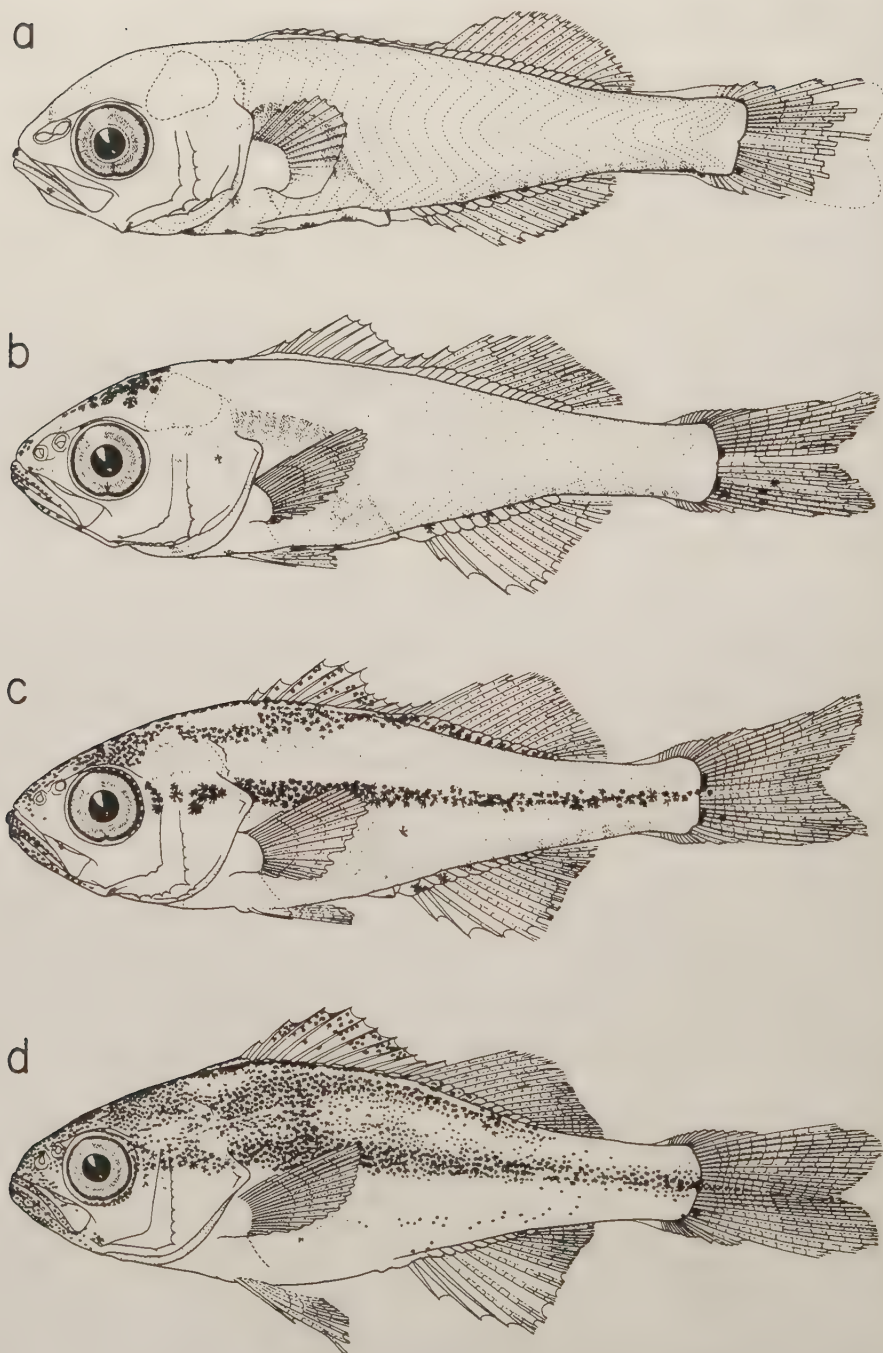


Figure 2. Larval (a, b), transforming (c), and juvenile (d) sargo, *Anisotremus davidsonii*: a. 8.5 mm (SIO 91-135); b. 12.6 mm (SIO 64-249); c. 17.2 mm (SIO 64-249); d. 24.9 mm (SIO 62-346).



Figure 3. Larval (a, b) and transforming (c) sargo, *Anisotremus davidsonii*, in dorsal view: a. 8.5 mm (SIO 91-135); b. 12.6 mm (SIO 64-249); c. 17.2 mm (SIO 64-249).

dorsal pigmentation increases rapidly: by 17.2 mm pigmentation is continuous along the dorsal margin to the dorsal fin insertion (Fig. 3c), extending up along the dorsal fin ray bases and onto the membranes between most of the dorsal fin spines (Fig. 2c). In addition, by ca. 17 mm a diagonal band of melanophores extends from the otic region to the middle of the spinous dorsal fin, and a stripe extends along the lateral midline to the end of the peduncle (Fig. 2c). The diagonal band subsequently broadens and extends posteriorly, and together with melanophores proliferating upward from the lateral midline, covers most of the upper half of the trunk and tail to the last dorsal ray by ca. 25 mm (Fig. 2d).

External pigment over the lateral gut region develops in the postflexion stage (Fig. 2a). This initially (ca. 8.2 mm) consists of a single melanophore just below the lateral midline at the level of the posterior end of the swimbladder. Melanophores subsequently are added over the entire lateral surface of the abdomen. A few ventrolateral tail melanophores, more-or-less continuous with the external gut pigment, develop during the early juvenile stage (Fig. 2c, d).

The gut is always pigmented dorsally (including pigment over the swimbladder), anteriorly, and externally along the ventral midline. During the preflexion stage dorsal gut pigment consists of one melanophore just anterior to the swimbladder (present in 89%), pigment on the dorsum (87%) or dorsum and posterior surface

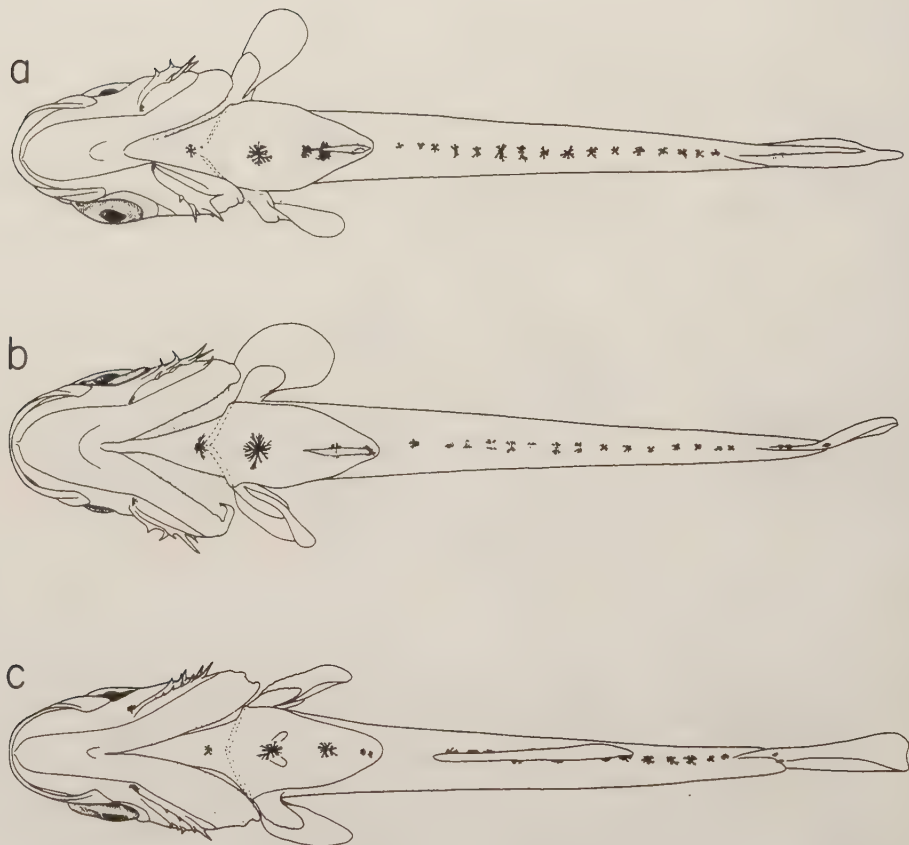


Figure 4. Larval sargo, *Anisotremus davidsonii*, in ventral view (all SIO 91-135): a. 4.1 mm; b. 4.9 mm; c. 7.2 mm.

(13%) of the swimbladder, and one to four (mode = 1) melanophores dorsally on the hindgut. Pigment spreads downward over the dorsolateral surfaces of the swimbladder during notochord flexion. The pigment on the dorsal surface of the hindgut extends anteriorly to the swimbladder and posteriorly to near the anus during flexion and postflexion stages. Pigment nearly always is present anteriorly adjacent to the liver (present in 87% of preflexion, 95% of flexion, and 100% of postflexion stage specimens); this typically is a single large melanophore.

Ventral pigment on the gut consists of one to six external melanophores (mode = 3) about evenly-spaced along the midline from the anterior midgut to the posterior hindgut. The midgut pigment always is present but about 25% of the specimens lacked the hindgut pigment. When pelvic fins develop, the first melanophore in this ventral series lies at the pelvic base.

Internal lateral pigment begins to develop over the dorsolateral gut region at ca. 8.2 mm. This pigmentation rapidly proliferates, so that by the end of larval development scattered internal melanophores cover nearly the entire gut area.

Head pigmentation during the preflexion and flexion stages is largely restricted to a melanophore under the hindbrain, one at each angular, and one on the isthmus

Table 1. Summary of measurements (in mm) of *Anisotremus davidsonii*. Body lengths are notochord length for preflexion and flexion-stage larvae, and standard length for postflexion and juvenile specimens. Measurements of body parts are summarized over 1 mm size classes; for each summary the mean measurement ($\bar{x}$), standard deviation (SD) and number of specimens measured (N) is given. Most specimens between dashed lines are undergoing notochord flexion (actual range undergoing flexion is 4.2–6.0 mm); specimens below the dotted line are juveniles

Body length (mm)	Snout length			Eye diameter			Head length			Pre-Anus length			Pre-Dorsal fin length			Pre-Anal fin length			Body depth			Longest pre-opercular spine		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
2.0–2.9	0.1	0.04	8	0.3	0.03	9	0.7	0.1	9	1.2	0.1	9							0.6	0.1	9	0.03	0.03	8
3.0–3.9	0.2	0.1	27	0.3	0.04	27	0.9	0.1	27	1.5	0.2	27							0.8	0.1	27	0.1	0.02	27
4.0–4.9	0.3	0.1	25	0.4	0.04	25	1.2	0.1	25	1.9	0.2	25	2.2	0.2	6	2.3	0.2	16	1.0	0.1	25	0.1	0.01	25
5.0–5.9	0.5	0.1	12	0.6	0.04	12	1.7	0.2	12	2.6	0.3	12	2.5	0.4	8	2.9	0.2	7	1.4	0.1	12	0.1	0.01	12
6.0–6.9	0.6	0.1	14	0.7	0.04	14	2.1	0.2	14	3.2	0.1	14	2.4	0.2	14	3.5	0.1	7	1.7	0.1	14	0.1	0.02	14
7.0–7.9	0.7	0.03	10	0.7	0.04	10	2.3	0.2	10	3.5	0.2	10	2.6	0.1	10	3.9	0.2	7	1.8	0.1	10	0.1	0.02	10
8.0–8.9	0.8	0	2	0.8	0.1	2	2.7	0	2	4.2	0.1	2	2.9	0.03	2	4.5	—	1	2.2	0.1	2	0.1	0.01	2
9.0–9.9	0.7	—	1	0.7	—	1	3.0	—	1	4.3	—	1	3.4	—	1	4.5	—	1	1.8	—	1	0.1	—	1
12.0–12.9	1.2	—	1	1.2	—	1	4.5	—	1	6.9	—	1	4.5	—	1	6.9	—	1	3.4	—	1	0.1	—	1
17.0–17.9	1.7	0.1	3	1.8	0	3	6.1	0.2	3	9.6	0.2	3	6.2	0.3	3	9.8	0.3	3	5.3	0.04	3	0.1	0.02	3
19.0–19.9	1.7	0.1	2	1.8	0.1	2	6.6	0.3	2	10.8	0	2	6.8	0	2	11.2	0.1	2	5.7	0	2	0.04	0.06	2

near the cleithral symphysis (present in 69% of preflexion, 97% of flexion, and all postflexion stage specimens). Apart from the isthmus melanophore, head pigment is entirely lacking in specimens smaller than 3.3 mm, and is present under the hindbrain in 7% and on the angular in 30% of the remaining preflexion stage specimens. The ventral hindbrain and angular pigment are present in 81% and 100%, respectively, of flexion and postflexion stage specimens.

An internal melanophore at the anterior margin of the forebrain, developing as early as ca. 6.4 mm, is present in 18% of postflexion specimens smaller than 7.2 mm and in 100% of larger larvae. One or two smaller melanophores may develop along the anterior margin of the forebrain, beginning at ca. 8.2 mm. External pigment may develop over the forebrain as early as 7.8 mm, but usually is absent in specimens smaller than ca. 9 mm. External pigment becomes dense over the fore- and midbrain region by ca. 12.6 mm and extends both anteriorly and posteriorly to completely cover the top of the head by 17.2 mm. This pigment is continuous dorsally with both the dorsal margin pigment and the anterior diagonal band, and ventrally with anterior premaxillary, dentary, and gular pigment.

Internal pigment may develop along the anterior sides of the hindbrain as early as 8.2 mm, but usually is absent until after ca. 9 mm. The hindbrain pigment becomes rather dense early in the juvenile stage, spreading onto the posterior region of the midbrain by 17.2 mm and nearly surrounding the brain in larger specimens.

Morphology.—The smallest sargo larva examined (2.2 mm) showed no evidence of yolk or oil droplet. At this size the eye is pigmented, the mouth is functional, the swimbladder is inflated, and the gut is tubular and folded into a broad "S" shape. The fold tightens, forming a coil in the midgut between 2.9 and 3.2 mm. Notochord flexion begins between 4.2 and 4.7 mm and is completed between 6.0 and 6.2 mm. Transformation to the juvenile stage (indicated by scale formation, which is anterior to posterior) begins at ca. 14–15 mm and is complete by ca. 19–22 mm.

Larval development is a gradual process with no marked changes in body proportions (Figs. 1, 2; Table 1). Snout length, head length, pre-anus length, and body depth all increase slightly relative to standard length (SL) during larval life. Snout length averages 7% of SL (range 4–9%) during the preflexion stage, increases to 9% (range 7–10%) during notochord flexion and to 10% (range 8–13%) in the postflexion stage. Mean proportions (and ranges) for head length are: preflexion stage 27% (22–31%), flexion stage 30% (26–34%), and postflexion stage 33% (28–36%). Respective values for pre-anus length are 45% (41–51%), 46% (37–50%), and 49% (46–55%); and for body depth 24% (19–26%), 25% (20–29%) and 26% (24–28%). Pre-dorsal fin length decreases as the fin develops, from 47% (range 36–53%) of SL during notochord flexion to 36% (range 33–39%) in postflexion larvae. Pre-anal fin length, on the other hand, remains 53% of SL (range 50–60%) during notochord flexion, 51–56% following flexion. Eye diameter likewise remains 10% of SL (range 8–11% over all stages) throughout larval development.

Skeletal Development.—Skeletal development of sargo closely resembles that of *Anisotremus virginicus*, described by Potthoff et al. (1984). Since Potthoff et al. (1984) provided good descriptions of development of the hyoid and branchial arches and axial skeleton of *A. virginicus*, descriptions of these in sargo are limited to figures, tables, listings of the few differences from *A. virginicus*, and in some cases, brief supplemental descriptions. Development of the neurocranium, jaws,

Table 2. Summary of skeletal development of *Anisotremus davidsonii*: size (mm SL) of smallest cleared and stained specimen with given structure visible as cartilage, or beginning to ossify; D = dermal origin

Structure	Size at first appearance of	
	Cartilage	Ossification
Neurocranium		
Basioccipital		4.2
Exoccipital		4.2
Parasphenotic		3.5
Pterosphenotic		8.7
Basisphenotic		14.9
Vomer		6.6
Lateral ethmoid		5.5
Median ethmoid	D	12.4
Lachrymal	D	7.1
Circumorbital 2	D	14.9
3	D	12.4
4	D	12.4
5	D	12.4
Dermosphenotic	D	14.9
Frontal	D	5.0
Parietal	D	6.6
Supraoccipital	D	6.6
Sphenotic		6.6
Pterotic		5.4
Prootic		4.5
Epitotic		5.5
Nasal	D	8.7
Jaws and suspensorium		
Premaxillary		2.9
Maxillary		2.9
Dentary		2.9
Articular	2.9	3.9
Angular	2.9	3.9
Hyomandibular	2.9	4.2
Symplectic	2.9	4.2
Quadrate	3.5	4.2
Ectopterygoid	4.2	4.6
Mesopterygoid	4.2	4.2
Metapterygoid	4.2	8.4
Palatine	4.6	5.7
Opercular series		
Preopercular	D	2.9
Opercular	D	2.9
Subopercular	D	4.2
Interopercular	D	4.2
Hyoid arch		
Branchiostegal	D	4.2
Ceratohyal	2.9	4.2
Epihyal	2.9	4.2
Interhyal	3.5	4.2
Ventral hypohyal	3.5	4.6
Dorsal hypohyal	3.5	5.7
Urohyal	D	4.2
Basihyal	5.4	8.7
Branchial arches		
Ceratobranchial	2.9	4.2
Epibranchial	3.5	4.2

Table 2. Continued

Structure	Size at first appearance of	
	Cartilage	Ossification
Hypobranchial	4.2	5.5
Basibranchial	3.5	5.5
Pharyngobranchial	3.5	5.7
Axial skeleton		
Vertebral centra		4.5
Urostyle		5.5
Neural arches	4.2	4.7
Haemal arches	4.2	4.7
Neural spines	4.2	5.7
Haemal spines	4.2	12.4
Epipleural ribs	D	12.1
Pleural ribs	8.7	12.1
Epurals	4.7	12.4
Hypurals 1-4	4.2	5.5
Hypural 5	7.1	8.7
Parhypural	4.2	7.1
Uroneurals		12.4
Caudal distal radials	12.9	
Dorsal pterygiophores	5.7	
Proximal radials	7.1	8.7
Distal radials	7.1	8.7
Anal pterygiophores	5.7	
Proximal radials	7.1	8.7
Distal radials	7.1	8.7
Pectoral and pelvic girdle		
Cleithrum		2.9
Supracleithrum	D	4.5
Dorsal postcleithrum	D	5.5
Ventral postcleithrum	D	4.7
Posttemporal	D	4.5
Supratemporals	D	12.4
Scapula	4.2	7.1
Coracoid	4.2	5.7
Pectoral proximal radials	6.7	12.4
Pectoral distal radials	14.4	
Basipterygia	8.7	12.4

and suspensorium of sargo are described in more detail, since Potthoff et al. (1984) did not deal with these structures in *A. virginicus*.

Initial ossification of each bone is visible as a very thin, hyaline layer forming on (or in) the corresponding cartilage or other tissue. This ossifying layer stained very lightly or not at all. Thus, a degree of uncertainty (probably ≤ 0.5 mm) should be assumed in the following descriptions of size at the beginning of ossification of each bone.

Neurocranium (Fig. 5, Table 2). — **CHONDROCRANIUM.** The chondrocranium of the smallest stained specimen (2.9 mm) consists of a small ethmoid plate, anteriorly fused trabeculae cranii, and the anterior and ventral parts of the auditory capsule (including a short anteriorly-directed postorbital process). The ethmoid plate subsequently broadens, and by 4.2 mm a dorsal process, the nasal septum, begins to extend from its anterior surface. Simultaneously, the laminae orbitonasalis begin to extend upward on each side from the lateral margin of the ethmoid plate,

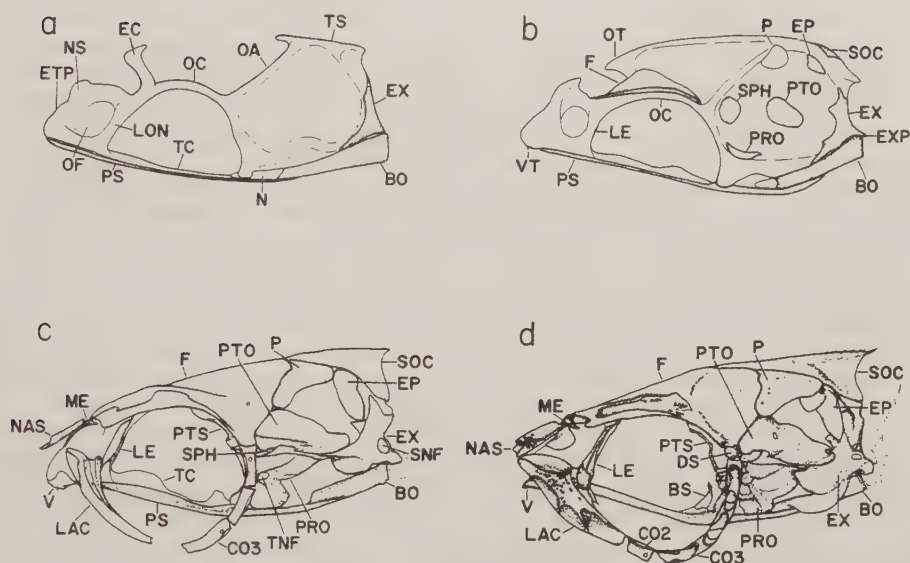


Figure 5. Lateral view of the developing neurocranium of sargo, *Anisotremus davidsonii*: a. 4.2 mm (SIO 91-135); b. 6.7 mm (SIO 91-135); c. 14.9 mm (SIO 91-136); d. 23.6 mm (SIO 62-346). White = cartilage; stippled = ossifying. Abbreviations are: BO = basioccipital; BS = basisphenotic; CO = circumorbitals; DS = dermosphenotic; EC = epiphysial cartilage; EP = epiotic; ETP = ethmoid plate; EX = exoccipital; EXP = posterior exoccipital process; F = frontal; LAC = lacrymal; LE = lateral ethmoid; LON = lamina orbitonasalis; ME = median ethmoid; N = notochord; NAS = nasal; NS = nasal septum; OA = occipital arch; OC = orbital cartilage; OF = olfactory foramen; P = parietal; PRO = prootic; PS = parasphenotic; PTO = pterotic; PTS = pterospheotic; SNF = foramen of first spinal nerve; SOC = supraoccipital; SPH = sphenotic; TC = trabecula communis; TNF = foramen of trigeminofacialis nerve; TS = synotic tectum; V = vomer; VT = vomerine tooth.

meeting the nasal septum between 4 and 4.5 mm, to define the olfactory foraminae. The orbital cartilages are complete at their first appearance (ca. 4 mm); each is fused anteriorly with the lamina orbitonasalis and posteriorly with the postorbital process of the auditory capsule, which itself is complete by ca. 4 mm. At this same size, the epiphysial cartilage, which bridges dorsally between the orbital cartilages, and the broad synotic tectum, which bridges dorsally between the auditory capsules, first appears in nearly final form. A narrow medial strip of cartilage bridges longitudinally between the epiphysial cartilage and the synotic tectum at ca. 4.6–4.8 mm. The trabeculae cranii are fused and a broad parachordal cartilage is present by ca. 4.5 mm. The chondrocranium apparently changes little subsequently, except that the trabecula communis separates into anterior and posterior parts, after 14.4 mm but before 17.9 mm. By ca. 20 mm the former trabecula consists anteriorly of a very short cartilaginous stub, and posteriorly of a cartilaginous foundation for the basisphenotic.

FRONTAL. The frontals first appear at ca. 5 mm (the frontals were ossifying in a single 4.3 mm specimen, but apparently were not ossifying in the other specimens <5 mm). Initially, each is a small, thin, elongate and somewhat oval dermal ossification above the eye. Subsequently, the frontals expand mesially, posteriorly, and to a lesser extent anteriorly, meeting along their mesial edges by ca. 7–8 mm. A supraocular shelf develops along the exterior edge of each between 6–6.5 mm. This shelf forms a U-shaped trough (open dorsally) during postflexion, and between ca. 14.5 and 20 mm the trough begins to close, from anterior to posterior,

to form part of the supraorbital canal of the laterosensory system. There are no supraocular spines. The frontals are very thin throughout larval development: the chondrocranium is easily seen through the frontals to at least 20 mm.

PARIETAL. Small, thin, oval parietals are first visible in the angle between the auditory capsule and synotic tectum at 6.5–7 mm. Each enlarges, primarily ventrad and slightly caudad, becoming roughly T-shaped by ca. 12.5–14.5 mm. Each parietal abuts against the supraoccipital and adjacent frontal by ca. 8.5–9 mm, abuts against (or slightly overlaps) the adjacent epiotic between ca. 12 and 18 mm, and overlaps the edge of the supraoccipital by ca. 14.5 mm.

BASIOCCIPITAL, EXOCCIPITAL, SUPRAOCCIPITAL. The basioccipital and exoccipital apparently are the second neurocranial elements to begin ossifying, by ca. 4 mm (Table 2). The basioccipital initially is a thin ossification around the notochord. Beginning at ca. 6.5 mm, a pair of very thin flanges extend laterally from its dorsolateral surfaces. Each soon becomes a shallow cup-like structure that forms the lower third of the saccular capsule.

The exoccipitals initially are thin, somewhat crescent-shaped ossifications along the dorsolateral surfaces of the posterior third of the basioccipital, continuing dorsad along the margins of the foramen magnum. Subsequent ossification dorsad and anteriad results in large, complex bones that form most of the posterior neurocranium and encircle all but the floor of the foramen magnum. The lateral wing of each exoccipital forms the roof of the saccular capsule. A posterior process of each exoccipital, first visible at ca. 4.5 mm, articulates with the first vertebral centrum. This process extends to about mid-way along the centrum (reached by ca. 14.5 mm). A thin process arising (ca. 9 mm) from the dorsal margin of the posterior exoccipital process bridges to the posterior margin of the ascending wing of the exoccipital by ca. 12.5–14.5 mm to define the first spinal nerve foramen.

The supraoccipital is first visible at ca. 6.5 mm as a very thin sliver of bone, medially above the posterior half of the synotic tectum. It first lengthens, and a crest begins to form (ca. 8.5–9 mm). The crest becomes triangular and rather large by ca. 14.5 mm, and serrate along its dorsal margin by ca. 20 mm. The supraoccipital expands laterally beginning at ca. 9–12 mm, forming a cap over the posterodorsal neurocranium. The supraoccipital abuts against the frontals at ca. 8.5–9 mm, is slightly overlapped by the parietals by ca. 14.5 mm, abuts against the epiotics by ca. 20 mm, and begins to form an interdigitating joint mesially with the exoccipitals in the largest cleared and stained specimen (23.6 mm).

BASISPHENOTIC, PARASPHENOTIC, PTEROSPHENOTIC, SPHENOTIC. A long, slender parasphenotic ossification, lacking ascending wings, lies along the ventral margin of the ethmoid plate and trabecula communis by ca. 3.5 mm. The ascending wings first appear as short stubs by ca. 4.5 mm, and extend to just below the trigeminofacialis foramen in the prootic by ca. 12.5–14.5 mm. A Y-shaped fork at the posterior end of the parasphenotic extends ventrolaterally on the basioccipital beginning at ca. 4 mm.

The sphenotic is first visible at ca. 6.5 mm as a small, thin, circular ossification just posterior to the junction of the orbital cartilage and auditory capsule. It remains essentially unchanged, until ca. 12.5 mm, when a small, laterally-directed flange develops on its lower surface. This flange first extends diagonally across the lower part of the sphenotic, then develops a short ascending section along the lower anterior sphenotic margin. Finally, the flange grows upward along its distal margin, to form a trough which receives the lower end of the dermosphenotic (ca. 20 mm).

The pterosphenotics begin to ossify by ca. 8.5 mm. Each initially is a thin, slender, crescent-shaped ossification posteriorly along the margin of the orbital

cartilage, and subsequently lengthens and extends posterolaterally to articulate with the frontal, sphenotic, and prootic by ca. 10 mm. The pterosphenotics remain thin and lightly ossified, except in a thin, well-ossified strip along the anterior margin, in the largest specimen stained (23.6 mm).

The basisphenotic begins to ossify at ca. 14.5 mm. It is located medially above the parasphenotic, just anterior to its ascending wings, on a cartilaginous base that apparently is the posterior remnant of the trabecula communis. The basisphenotic does not articulate directly with any other bone in the cleared and stained specimens.

VOMER. The vomer first appears at ca. 6.5 mm as two separate, very thin, slender ossifications on the anterolateral margins of the ethmoid plate. Each ossification is centered around a small vomerine tooth. By ca. 8.5 mm the two vomerine ossifications have joined across the anterior margin of the ethmoid plate, forming a thin, crescent-shaped vomer. Subsequent ossification results in a T-shaped vomer by ca. 12.5 mm; the two vomerine teeth persist to at least 14.4 mm, but are not visible in juveniles (apparently absent by ca. 20 mm).

EPIOTIC, PROOTIC, PTEROTIC. Each of these is first visible between ca. 4.5 and 5.5 mm (Table 2), as a small, thin, oval ossification. The prootic and pterotic apparently begin ossifying slightly before the epiotic. The prootics expand rapidly and substantially, forming much of the floor of the brain case by the end of the larval stage. Each articulates with the sphenotic and pterotic by ca. 8.5 mm, with the exoccipital and ascending wing of the parasphenotic by 12.5–14.5 mm, and is separated from the pterosphenotic only by a thin strip of cartilage by ca. 22.5 mm. The foramen for the trigeminofacialis nerve is a prominent feature from ca. 8.5 mm onward. The pterotic quickly expands, primarily longitudinally, becoming distinctly oval by 6.5 mm. It overlaps the sphenotic by ca. 13 mm and reaches the posterior margin of the frontal by 14.4 mm. A low longitudinal ridge arises from the lateral surface of the pterotic beginning by ca. 13 mm: this is the lower margin of the pterotic canal of the laterosensory system, which is formed by ca. 23.5 mm. The epiotics expand, primarily ventrad, becoming elongate ovals by ca. 8.5 mm and, together with the exoccipitals, form most of the posterior neurocranium by ca. 20 mm. The epiotics abut against the supraoccipital by ca. 13–14.5 mm, overlap the exoccipitals by ca. 20 mm, and are overlapped along their anterodorsal margin by the parietals, at ca. 22.5–23.5 mm.

LATERAL ETHMOID, MEDIAN ETHMOID. The lateral ethmoids begin to ossify between 4.7 mm and ca. 5.5 mm. Each initially appears as a thin, slender ossification along the posterior margin of the lamina orbitonasalis, and subsequently expands dorsally, ventrally, and laterally, to form a shallow U-shaped ossification around the posterior half (approximately) along most of the length of the lamina orbitonasalis, by ca. 12 mm. A mesial flange develops along the lower half of each lateral ethmoid beginning ca. 14.5 mm, but the two mesial flanges remain widely separated in the largest cleared and stained specimen. Each lateral ethmoid reaches the adjacent frontal at about 14.5 mm, and articulates with the adjacent lacrymal by ca. 22.5 mm. A short tube, through which the olfactory nerve passes, develops on the upper anterior surface of the lateral ethmoid at ca. 22.5–23.5 mm.

The median ethmoid first appears at ca. 12.5 mm as a thin, slender ossification along the anterodorsal margin of the nasal septum. Lateral wings begin to develop near its upper end at ca. 13 mm, so that it becomes roughly T-shaped in dorsal view. Subsequent lateral expansion results in the median ethmoid becoming somewhat pear-shaped (in dorsal view), with the lateral wings extending from the narrower upper end. The median ethmoid meets the anterior margins of the frontals by ca. 20 mm.

NASAL. The nasals, which begin to ossify by ca. 8.5 mm, first appear as small, thin, U-shaped dermal bones just above and lateral to the nasal septum. They become larger and somewhat more deeply U-shaped, but otherwise change little through the end of larval development. In early juveniles, each nasal closes dorsally, beginning at the anterior end, to become a tube (ca. 20–22.5 mm) at the anterior end of the laterosensory canal system.

CIRCUMORBITALS. The lacrymal is the first circumorbital bone to develop, beginning between ca. 7–8.5 mm. In the 8.2 mm cleared and stained specimen, it is a flat, somewhat triangular bone, with a narrow lateral flange along its anterolateral edge. This flange expands and grows upward; at ca. 22.5–23.5 mm it meets a second lateral flange that arises (ca. 13–14.5 mm) from the lateral surface of the lacrymal, to form a low, oval tube. Concurrently, the lacrymal enlarges substantially, extending at its dorsal margin (by ca. 22.5 mm) from the level of the posterior margin of the lateral ethmoid to just beyond the anterior end of the ethmoid plate. The upper part of the lacrymal becomes somewhat cup-shaped at its posterior end, where it articulates with the lower end of the lateral ethmoid. Circumorbitals 3–5 apparently begin ossifying more-or-less simultaneously, at ca. 12.5 mm. Each initially is a thin, flat to shallowly U-shaped dermal ossification; by ca. 23.5 mm all are becoming tubular. Circumorbital 2 and the dermosphenotic are the last to form, at ca. 14.5 mm. In the largest cleared and stained specimen, circumorbital 2 is a shallow U-shaped bone, and the dermosphenotic is an essentially flat oval-shaped bone that is inserted along its lower margin into the lower sphenotic.

Jaws and Suspensorium (Fig. 6, Table 2). — **MAXILLARY, PREMAXILLARY, ROSTRAL CARTILAGE.** In the smallest cleared and stained specimen (2.9 mm) the upper jaw consists of a pair of long, slender maxillaries and a pair of very small, more-or-less triangular premaxillaries, each with a single tooth. The maxillaries quickly broaden, more so distally. Each develops a short anterior process near its anteroventral margin; this process extends laterally to just beyond the posterior margin of the premaxillary by ca. 4 mm. A short dorsal process develops simultaneously at the same level. Both processes subsequently broaden, and the dorsal process forms an inverted "U" whose legs diverge ventrad, with the mesial leg extending to the anteroventral margin of the ethmoid plate by ca. 8.5 mm. A thin, posteriorly-directed flange arising from the interior margin of the ascending process of the premaxillary fits loosely into the inverted U of the maxillary, to form a tongue and groove-like joint by ca. 8.5 mm.

A short ascending process and a long, slender posterior process bearing three teeth develop on each premaxillary by 4.2 mm. The premaxillaries subsequently broaden, with the posterior process of each broadening much more, to form a flat crescent-shaped flange (by ca. 6.5 mm) that extends dorsad, mesial to the maxillary, reaching well past the upper maxillary margin by ca. 20 mm (Fig. 6d).

The rostral cartilage, a large, oval cartilage first visible at ca. 5.5–6.5 mm, lies between the premaxillary ascending processes. The ascending processes reach three-quarters of the way up its length at 6.5 mm, and the posterior premaxillary flanges reach about one-third up each side by ca. 20 mm.

ANGULAR, ARTICULAR, DENTARY. The lower jaw of the smallest cleared and stained specimen consists of the paired Meckel's cartilages, which abut mesially at their anterior ends. A slender dentary ossification bearing two teeth lies along the anterodorsal margin of each. The dentaries soon deepen and extend posteriorly, each forming a Y-shaped articulation with the anterior end of the ossifying articular by ca. 4 mm. The dentary canal of the laterosensory system is first apparent at ca. 8–8.5 mm as a shallow groove along the lower lateral surface on

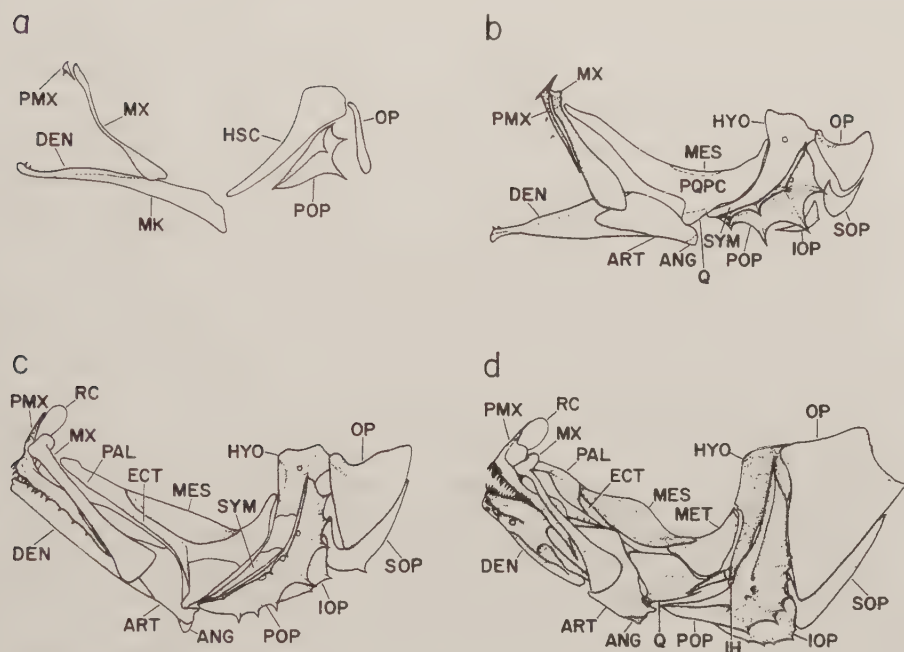


Figure 6. Development of the jaws, suspensorium, and opercular bones of sargo, *Anisotremus davidsonii*: a. 2.9 mm (SIO 91-135); b. 4.2 mm (SIO 91-135); c. 6.7 mm (SIO 91-135); d. 23.6 mm (SIO 62-346). White = cartilage; stippled = ossifying. Abbreviations are: ANG = angular; ART = articular; DEN = dentary; ECT = ectopterygoid; HSC = hyomandibulosymplectic cartilage; HYO = hyomandibular; IOP = interopercular; MES = mesopterygoid; MET = metapterygoid; MK = Meckel's cartilage; MX = maxillary; OP = opercular; PAL = palatine; PMX = premaxillary; POP = preopercular; PQPC = palato-ptyergoquadrate cartilage; Q = quadrate; RC = rostral cartilage; SOP = subopercular; SYM = symplectic.

the anterior half of the dentary. This groove closes to form a tube, from anterior to posterior, beginning by ca. 20 mm.

Each articular begins to ossify at ca. 4 mm, along the lower lateral face of the posterior half of Meckel's cartilage. Subsequent ossification is primarily dorsad and anterorad. By ca. 5 mm the anterior end of the articular extends anteriorly along the mesial surface of the dentary. A shallow notch, present on the postero-dorsal margin of Meckel's cartilage, becomes the socket for the articular condyle of the quadrate. A posterior projection, which nearly reaches the anterior end of the preopercular, extends from the posterior margin of the articular, beginning at ca. 6 mm.

The angular ossifies from the posteroventral corner of Meckel's cartilage, beginning at ca. 4 mm, and articulates with the posteroventral margin of the articular.

HYOMANDIBULAR, SYMPLECTIC. An undivided hyomandibulosymplectic cartilage is present in the smallest cleared and stained specimen. Hyomandibular ossification begins in the vicinity of the facial nerve foramen before 4 mm, extends dorsally and laterally to the margins of the sphenotic and pterotic condyles by 4.3 mm, and spreads ventrad after ca. 4 mm. The opercular condyle remains cartilaginous until ca. 8.5 mm.

The symplectic is first visible (ca. 4 mm) as a thin ossifying sheath around the

lower part of the hyomandibulosymplectic cartilage. Except for extending farther along the length of the cartilage and becoming more heavily ossified, it does not change. The symplectic articulations with the quadrate and hyomandibular remain cartilaginous in the largest cleared and stained specimen.

ECTOPTERYGOID, MESOPTERYGOID, METAPTERYGOID, PALATINE, QUADRATE. The pterygoid bones, palatine, and quadrate all ossify from a single cartilage, which is absent in the smallest cleared and stained specimen, but is forming by ca. 3.5 mm. This cartilage initially appears as an inverted triangle with short dorsal anterior and posterior processes which subsequently (by ca. 4 mm) elongate (e.g., Fig. 6b). The mesopterygoid, followed quickly by the quadrate, are first to begin ossifying at about 4 mm (Table 2). The mesopterygoid ossifies from the dorsal margin along the middle of the cartilage, while the quadrate begins ossifying along its ventral condyle and subsequently fans out over most of the lower limb of the cartilage. The ectopterygoid begins ossifying along the lower margin of the anterior process of the cartilage at ca. 4.6 mm. The anterior margin of the developing quadrate reaches the posterior margin of the ectopterygoid at ca. 6.5 mm and overlaps it by ca. 20 mm. At this size (20 mm) the posterior dorsal margin of the quadrate articulates with the metapterygoid, and a posterior projection begins to extend from the lower posterior margin of the quadrate. This projection is just ventrad (and external) to the lower margin of the symplectic, and by ca. 23.5 mm it extends (dorsad) along most of the length of the lower limb of the preopercular.

The mesopterygoid becomes a large, elongate oval (in dorsal view), slightly cupped bone that extends from the lower margin of the eye to about one-quarter of the way up its mesial surface, by ca. 22.5 mm. The mesopterygoid articulates with the ectopterygoid at ca. 7 mm, and with the palatine and metapterygoid between ca. 20–23.5 mm. The anterodorsal margin of the metapterygoid slightly overlaps the posteroventral mesopterygoid margin by ca. 23.5 mm. The mesopterygoid and quadrate remain separated by a narrow band of cartilage in the largest cleared and stained specimen.

Metapterygoid ossification begins around the upper end of the posterior limb of the palato-ptyergoquadrate cartilage at ca. 8.5 mm, and subsequently spreads down along the posterior limb to articulate with the quadrate and overlap the margin of the mesopterygoid. An interdigitating articulation between the upper end of the metapterygoid and the hyomandibular begins to form at ca. 23.5 mm. A posteriorly-projecting mesial metapterygoid flange (Johnson, 1980) does not develop by 23.6 mm (absent in all cleared and stained specimens).

The palatine is first visible at ca. 5.7 mm as a thin ossification along the anterior ventral margin of the palato-ptyergoquadrate cartilage. The palatine subsequently ossifies around the cartilage, and extends posteriorly to articulate with the mesopterygoid and ectopterygoid by 12.4 mm. The palatine articulations with the lateral ethmoids and maxillaries remain cartilaginous in the largest cleared and stained specimen. There are no palatine teeth.

Opercular Series (Fig. 6, Table 2).—The preopercular and opercular are present in the smallest cleared and stained specimen (2.9 mm). At this size the preopercular has two spines on the posterior margin of the interior shelf, and one (much smaller) spine on the margin of the narrower exterior shelf. The full complement of 7–8 spines along the interior shelf is present by ca. 6 mm, and persists to at least 23.6 mm. The middle spine in this series typically is a bit longer than the others. The exterior shelf acquires a maximum of three small spines by ca. 4–4.5 mm; these become smaller and blunt during postflexion, then disappear between 9.3 and 12.2 mm. At the end of the larval stage the posterior margin of the exterior shelf

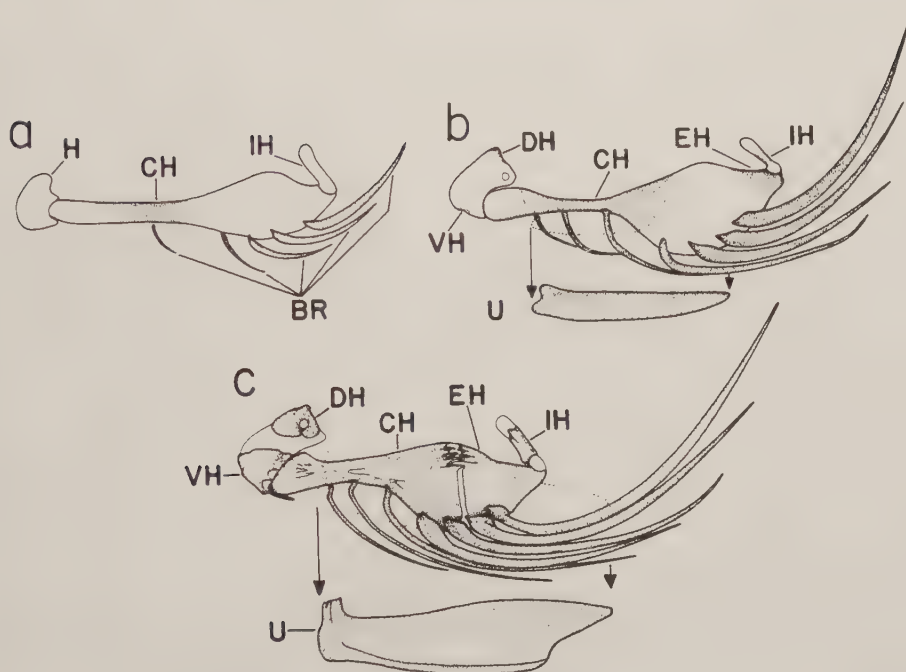


Figure 7. Development of the hyoid arch of sargo, *Anisotremus davidsonii*: a. 4.2 mm (SIO 91-135); b. 6.7 mm (SIO 91-135); c. 23.6 mm (SIO 62-346). White = cartilage; stippled = ossifying. Abbreviations are: BR = branchiostegals; CH = ceratohyal; DH = dorsal hypohyal; EH = epihyal; H = hypohyal cartilage; IH = interhyal; U = urohyal; VH = ventral hypohyal.

extends inward toward the interior shelf, and by ca. 20 mm it contacts the interior shelf midway along the length of the preopercular, forming part of the preoperculomandibular canal.

The opercular initially is a slender ossification extending from near the upper posterior margin of the hyomandibulosymplectic cartilage, along the upper posterior margin of the preopercular. It expands to a roughly triangular shape by ca. 4 mm, acquires a spine along the posterodorsal margin by ca. 8.5 mm, and may acquire a second, smaller spine near the top of the posterior margin by ca. 20 mm.

The subopercular and interopercular apparently begin forming simultaneously, at ca. 4 mm. The subopercular initially is a small, crescent-shaped dermal ossification just below the lower margin of the opercular. Subsequent changes consist largely of enlargement, and first acquiring, then losing, a spine along its lower margin (ca. 5–12 mm). The interopercular first appears as a slender blade-like dermal ossification with a single very small spine, just mesial to the middle of the posterior margin of the preopercular. It subsequently expands to become a broad, somewhat crescent-shaped bone, and acquires up to four more spines along its posterior margin by the end of the larval stage. The interopercular spines persist to at least 23.6 mm.

Hyoid Arch (Fig. 7, Table 2).—Development of the hyoid arch and branchiostegal rays in sargo is essentially identical to that described by Potthoff et al. (1984) for *Anisotremus virginicus*. Johnson (1980) noted that a ceratohyal beryciform fo-

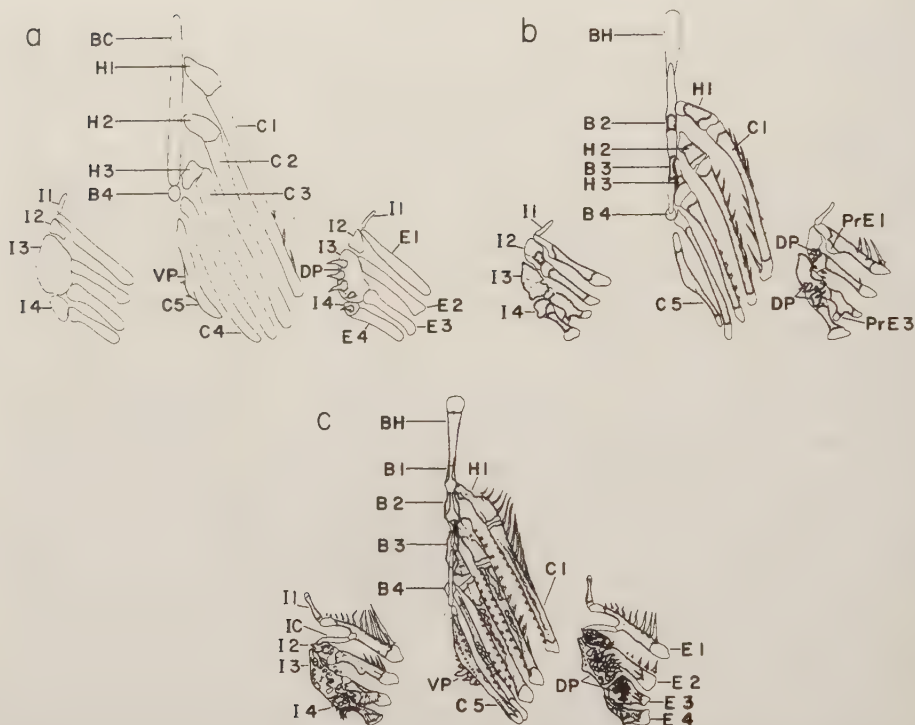


Figure 8. Development of the branchial arches of sargo, *Anisotremus davidsonii*: a. 4.2 mm (SIO 91-135); b. 6.7 mm (SIO 91-135); c. 23.6 mm (SIO 62-346). White = cartilage; stippled = ossifying. The left side of the branchial arches are shown in ventral view, with the epibranchials and dorsal tooth plates displaced laterally to the right in the figure. The right epibranchials and dorsal tooth plates are shown in dorsal view, displaced to the left in the figure. Abbreviations are: BC = basibranchial cartilage; B1-4 = basibranchials 1-4; C1-5 = ceratobranchials 1-5; DP = dorsal tooth plate; E1-4 = epibranchials 1-4; H1-3 = hypobranchials 1-3; IC = interarcual cartilage; I1-4 = pharyngobranchials 1-4; PrE1, 3 = process on epibranchials 1, 3; VP = ventral tooth plate.

ramen is present in the genus *Anisotremus*, and Potthoff et al. (1984, fig. 24) showed a feature that appeared to be this structure in juvenile *A. virginicus*; in sargo there is no evidence of the beryciform foramen in larvae or early juveniles (to 23.6 mm).

Branchial Arches (Fig. 8, Table 2).—Development of the branchial arches in sargo closely resembles that described for *A. virginicus* (Potthoff et al., 1984).

In sargo, basibranchials 2 and 3 may begin ossifying slightly before basibranchial 1 (e.g., Fig. 8b), in contrast to simultaneous ossification in *A. virginicus* (Potthoff et al., 1984). Tooth plates on epibranchials 2 and 3, present in a 21.5 mm specimen of *A. virginicus* (Potthoff et al., 1984), were not seen in sargo. The interarcual cartilage connecting epibranchial 1 with pharyngobranchial 2 apparently develops later (ca. 8.5 mm) in sargo than in *A. virginicus* (ca. 5.7 mm; Potthoff et al., 1984).

Axial Skeleton (Figs. 9, 10; Tables 2, 3).—**VERTEBRAL COLUMN** (Fig. 9). There are no neural or haemal arches or spines in the 2.9 mm larval sargo, but most are present as cartilage by ca. 4 mm. It could not be determined whether the arches develop from anterior, middle, and posterior sites along the notochord, as was

Table 3. Counts of fin spines and rays, vertebrae, ribs, gill rakers (outer arch: counts given as epibranchial, and hypobranchial + ceratobranchial; one raker at the ceratobranchial-epibranchial articulation is counted with the ceratobranchial rakers), and branchiostegal rays in *Anisotremus davidsonii*. Specimens between dashed lines are undergoing notochord flexion; those below the solid line are juveniles

Length (mm)	Fin rays				Vertebrae	Ribs		Gill rakers	Branchi- ostegal rays
	1°C	2°C	D	A	P ₁	P ₂	Pleural	Epipleural	
2.9									
3.5									
4.2	2+2								5
4.3	1+1								5
4.5	3+3								5
4.5	4+4								6
4.6	5+5					2			5
4.6	5+5					3			6
4.6	3+3					3			6
4.7	5+5					3			6
4.7	8+8					10+3			6L,7R
5.0	5+5					6			6
5.2	8+8					10+5			7
5.4	8+8					10+3			7
5.4	8+8					10+3			7
5.4	9+8					10+4			7
5.4*	9+8					10+13			7
5.5	8+8			8		10+4			6
5.5	9+8		6	5		10+9			7
5.7	9+8					10+8			7L,6R
5.7	4+4								6
5.8	9+8	0+1	11	8		10+9			7

Table 3. Continued

Length (mm)	Fin rays		A	P ₁	P ₂	Vertebrae	Ribs		Gill rakers	Branchi- ostegal rays
	1°C	2°C					Pleural	Epipleural		
6.7	9+8	0+1	II,10	4		10+16			3+8	7
7.1	9+8	1+2	II,10	5		9+15			0+10	7
7.1	9+8	2+2	I,12	6		10+16			2+10	7
7.9	9+8	2+2	X,15	8	I,2	10+16			2+10	7
8.2	9+8	4+4	XI,14	11	I,3	10+16			2+10	7
8.2	9+8	4+4	X,15	11		10+16			—	7
8.4	9+8	3+3	II,11	10	I,1	10+16			3+12	7
8.8	9+8	2+3	I,12	7	I,1	10+16			3+13	7
12.1	9+8	9+8	III,11	17	I,5	10+16	5	6	7+14	7
12.4	9+8	12+11	III,10	17	I,5	10+16	8	6	7+13	7
12.9	9+8	10+9	III,10	18	I,5	10+16	7	4	7+14	7
14.9	9+8	12+11	III,10	18	I,5	10+16	8	6L, 7R	6+15	7
17.9	9+8	11+10	III,9	18	I,5	10+16	8	8	7+16	7
19.9	9+8	12+11	II,9	17	I,5	10+16	8	9	9+16	7
22.6	9+8	14+12	III,10	18	I,5	10+16	8	9	9+15	7
23.6	9+8	13+13	III,10	19	I,5	10+16	8	8	9L, 11R+15	7

* Postflexion specimen, probably shrunken.

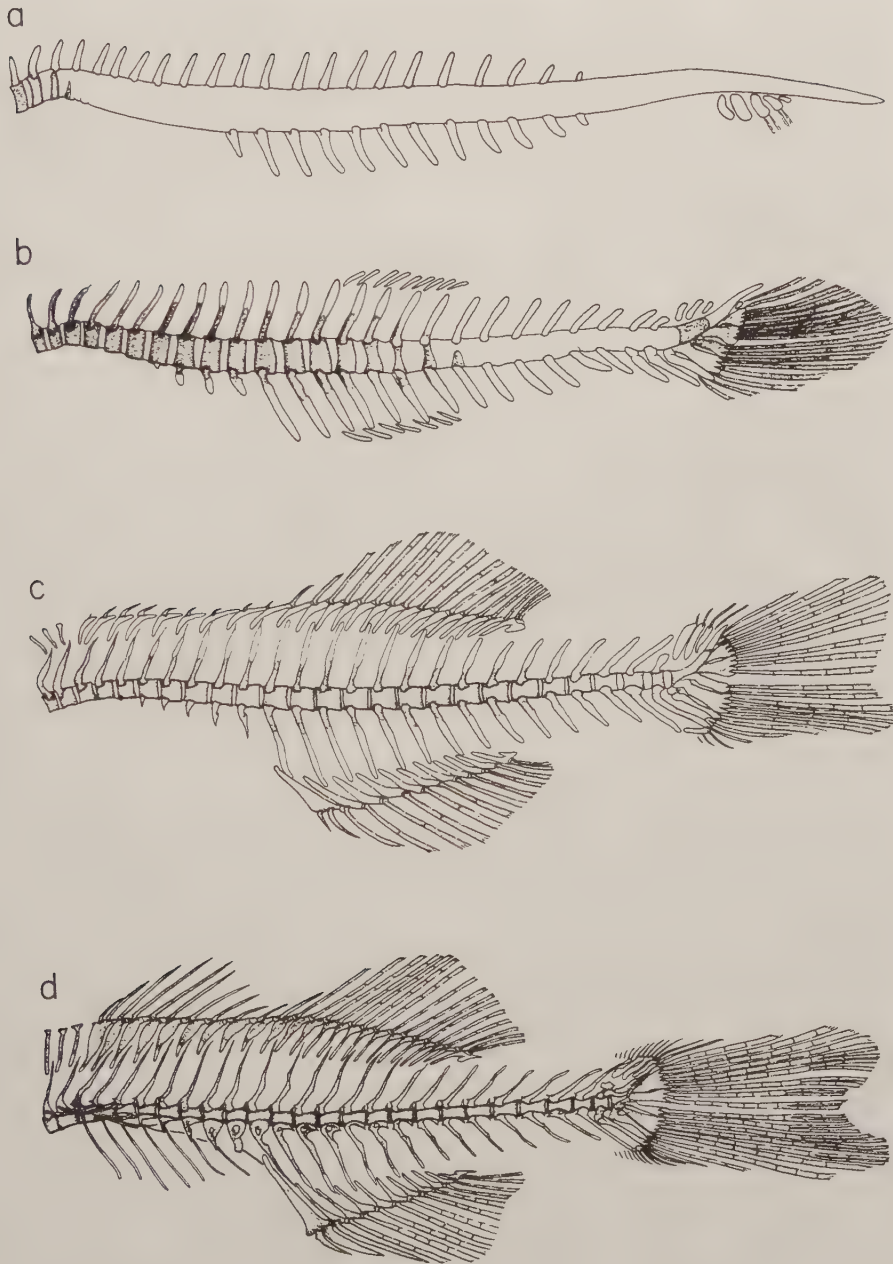


Figure 9. Development of the axial skeleton of sargo, *Anisotremus davidsonii*: a. 4.2 mm (SIO 91-135); b. 5.7 mm (SIO 91-135); c. 8.2 mm (SIO 91-135); d. 14.9 mm (SIO 91-136). White = cartilage; stippled = ossifying.

described for *A. virginicus* (Potthoff et al., 1984). Ossification of the arches and spines is anterior to posterior, and the arches on the abdominal vertebrae ossify distad from their bases in sargo as in *A. virginicus*. However, in contrast to *A. virginicus*, the arches on the caudal vertebrae in sargo apparently begin ossifying from just above their bases, and subsequently ossify both distad and proximad. Neural prezygapophyses develop on neural arches 3–25, and haemal prezygapophyses on haemal arches 11–25. These are first visible at 12.4 mm, on neural arches 3–23 and haemal arches 14–23.

Ossification of vertebrae begins at ca. 4.5 mm and is anterior to posterior, except that the urostyle ossifies before most caudal vertebrae. Each centrum begins ossifying as a thin ventral band between the proximal ends of its haemal arch. Ossification is dorsad from this ventral origin; when it has reached about one-third of the way up each side of the notochord, a dorsal saddle ossifies between the bases of the neural arch, then continues ventrad to meet the ascending arms of the ventral band. Neural postzygapophyses develop on centra 2–25, and haemal postzygapophyses develop on centra 10–23. These develop after 9.3 mm, and nearly all are present by 12.4 mm (neural postzygapophyses on centra 4–21 and haemal postzygapophyses on centra 10–21 in the 12.4 mm specimen). Neural and haemal postzygapophyses originate as small, laterally-paired, spine-like processes at the posterior dorsolateral and ventrolateral margins of each centrum, respectively. Low, thin, ossified flanges develop along each centrum, bridging from the "spines" to their adjacent (anterior) neural or haemal arches. These subsequently enlarge and acquire variable numbers and sizes of foramina.

PLEURAL AND EPIPLEURAL RIBS. Eight pleural and eight or nine epipleural ribs develop in sargo. Larvae ≤ 9.3 mm have none, but in the 12.4 mm specimen centra 3–9 support seven pleural ribs and centra 1–4 support four epipleural ribs. The pleural ribs develop from cartilage; the epipleural ribs are dermal ossifications originating in the myosepta.

CAUDAL FIN (Fig. 10). The first visible caudal elements (ca. 4 mm) are the cartilaginous parhypural, cartilaginous hypurals 1–4, and four calcified fin rays supported by hypurals 2 and 3. In contrast to apparently simultaneous development in *A. virginicus*, the haemal spines of preural centra 2 and 3 develop after the parhypural and hypurals (except hypural 5) in sargo. Both are present as cartilage by 4.3 mm. Ossification of hypurals 1–3 begins at ca. 5.5 mm. The parhypural apparently begins ossifying at ca. 7 mm. Uroneurals develop later in sargo than in *A. virginicus*: sargo 12.1 mm or smaller have none (both pairs are present in all larger specimens), while both pairs are present by 6.2 mm in *A. virginicus* (Potthoff et al., 1984). Sargo apparently acquires only two ventral distal radial cartilages, in contrast to three for *A. virginicus* (Potthoff et al., 1984). None of the cleared and stained specimens had a separate radial cartilage adjacent to the tip of the haemal spine of preural centrum 2 (present in *A. virginicus*), and the other two radial cartilages do not shift in location as they do in *A. virginicus* (Potthoff et al., 1984). A radial cartilage is present at the distal tip of hypural 5 in *A. virginicus* (Potthoff et al., 1984); none was seen in sargo, although in the 23.6 mm juvenile the cartilaginous distal tip of hypural 5 appears to have been just beginning to separate into proximal and distal elements.

DORSAL AND ANAL FINS. The first elements to form in the dorsal and anal fins might be the cartilaginous pterygiophores of the middle soft rays: the 5.7 mm specimen has these pterygiophores and lacks dorsal and anal fin rays, but a 5.5 mm specimen and all specimens 5.8 mm and larger have both the pterygiophores and fin rays. In the 5.7 mm specimen (Fig. 9b), the dorsal and anal pterygiophores are those that would have supported dorsal rays 5–13 and anal rays 2–8. In the

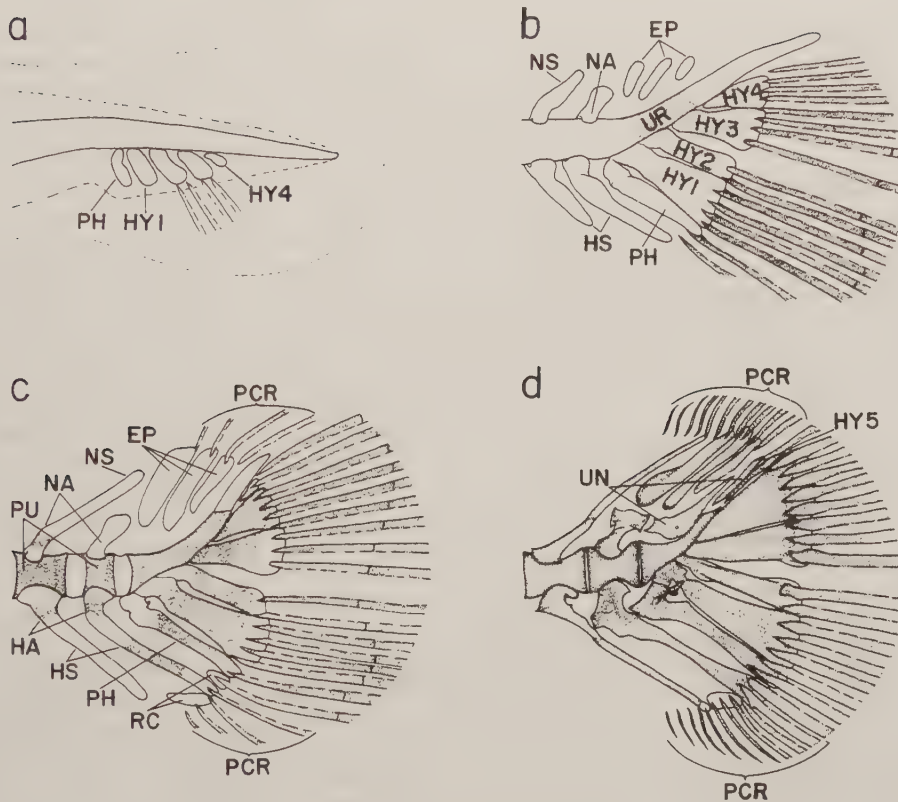


Figure 10. Development of the caudal skeleton of sargo, *Anisotremus davidsonii*: a. 4.2 mm (SIO 91-135); b. 5.5 mm (SIO 91-135); c. 8.2 mm (SIO 91-135); d. 14.9 mm (SIO 91-136). White = cartilage; stippled = ossifying. Abbreviations are: EP = epural; HA = haemal arch; HS = haemal spine; HY1-5 = hypurals 1-5; NA = neural arch; NS = neural spine; PCR = procurrent caudal ray; PH = parhypural; PU = preural centrum; RC = radial cartilage; UN = uroneural; UR = urostyle.

5.5 mm specimen, dorsal rays 5-10 and anal rays 2-6 are present already. Addition of pterygiophores is both anterior and posterior in the anal and second dorsal fins, and may be posterior to anterior in the first dorsal: only the posterior three dorsal spine pterygiophores are present at 6.6 mm, and all are present in specimens 6.7 mm and larger. Addition of soft rays is both anterior and posterior in both fins. Addition of dorsal spines begins anterior from the posteriormost spine; spines II-III or IV appear about simultaneously with spine IX or X, and then the middle spines probably are added from anterior to posterior. The first spine is added about simultaneously with spine IV or V. Development of the individual dorsal and anal pterygiophores, spines, and rays is the same as was described for *A. virginicus*, except that it is unclear whether both the second and third anal spines, or only the third, develop from rays in *A. davidsonii* (both the second and third spines develop from rays in *A. virginicus*: Potthoff et al., 1984). The first dorsal pterygiophore, which supports the first two spines, originates as two separate cartilages in sargo as in *A. virginicus*: these separate cartilages were seen in the 8.2 mm specimen (Fig. 9c). It could not be determined whether the first anal pterygiophore originates as one or two cartilages in sargo (there are two in *A.*

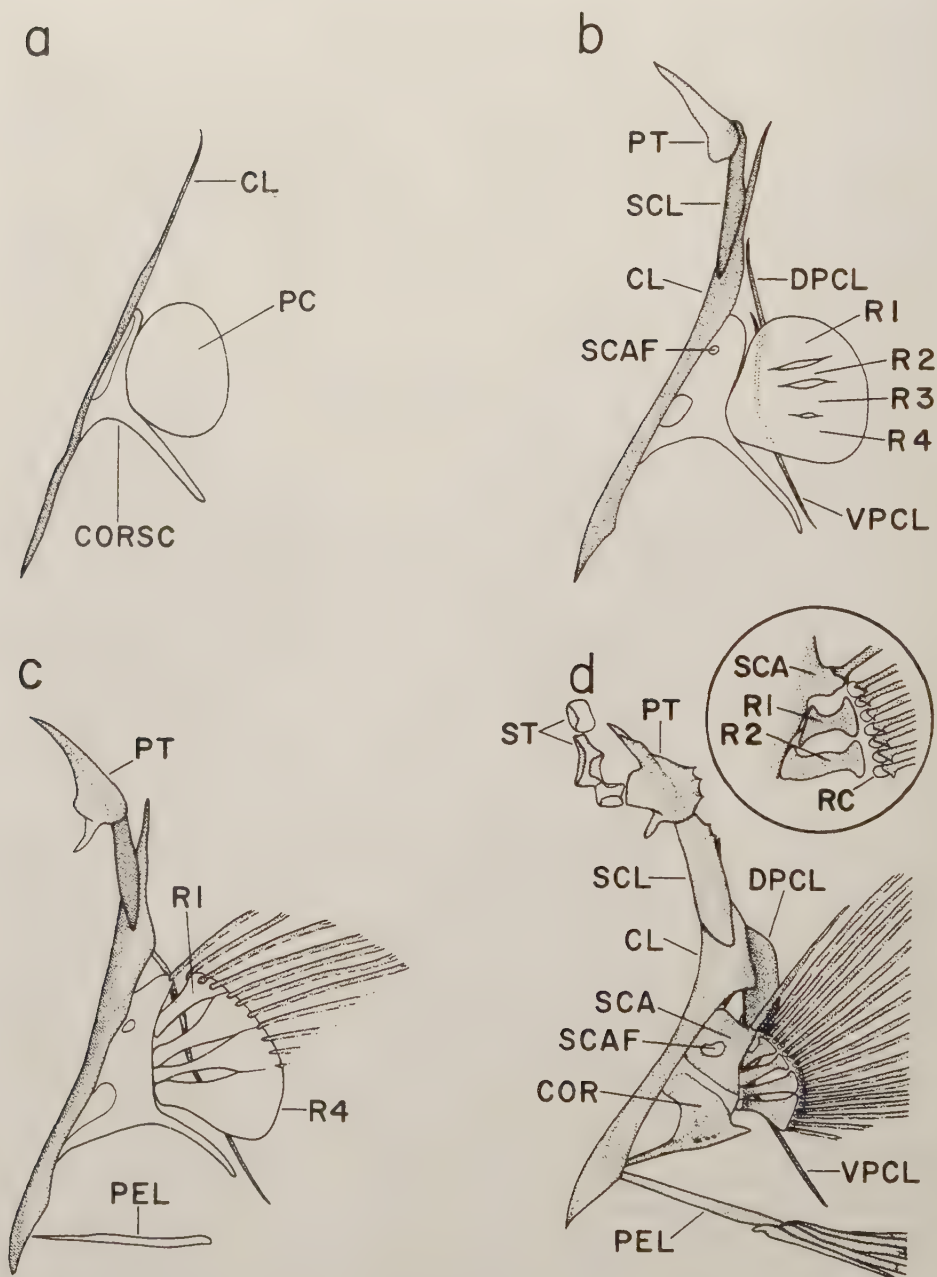


Figure 11. Development of the pectoral girdle of sargo, *Anisotremus davidsonii*: a. 2.9 mm (SIO 91-135); b. 6.7 mm (SIO 91-135); c. 8.2 mm (SIO 91-135); d. 14.9 mm (SIO 91-136). White = cartilage; stippled = ossifying. Abbreviations are: CL = cleithrum; COR = coracoid; CORSC = coracoscapular cartilage; DPCL = dorsal postcleithrum; PC = cartilaginous pectoral blade; PEL = pelvis; PT = post-temporal; RC = cartilaginous distal radial; R1-4 = proximal radials 1-4; SCA = scapula; SCAF = scapular foramen; SCL = supracleithrum; ST = supratemporal; VPCL = ventral postcleithrum.

virginicus). Separate cartilages were not seen in any specimen, but the 8.4 mm specimen had a large foramen (absent in all others) near the anterior distal margin of the pterygiophore, that nearly separated a thin, crescent-shaped anterior section from the remainder of the pterygiophore. This anterior section might have originated as a separate cartilage that was in the process of fusing with the principal part of the pterygiophore in the 8.4 mm specimen.

Pectoral and Pelvic Girdle (Fig. 11, Table 2).—Development of the pectoral and pelvic fins and their supporting bones is essentially the same in sargo as was described for *A. virginicus* (Potthoff et al., 1984). Initial development of the pectoral proximal radials could not be tracked in sargo. The 2.9 mm specimen has an undivided pectoral cartilage (Fig. 11a), while the 6.7 mm specimen has all three cleavages that define the four radials (Fig. 11b). The pectoral blade or radial cartilages did not stain with alcian blue in any of the intermediate-size specimens. Ossification of the proximal radials apparently begins later in sargo than in *A. virginicus*: none were ossifying through 9.3 mm, but radials 1–3 were ossifying in the 12.4 mm specimen, and all four were ossifying by 14.4 mm, in contrast to ossification beginning between 8.6–10.4 mm in *A. virginicus*. The cartilaginous distal pectoral radials were first seen at 14.4 mm. Supratemporal bones were not visible in specimens 9.3 mm or smaller, but were well developed in all specimens 12.4 mm and larger.

Xenistius californiensis

Pigmentation (Figs. 12–15).—Salema is lightly pigmented throughout most of the larval stage, closely resembling sargo during the preflexion stage. During preflexion 14 to 22 melanophores (mode = 16), usually of similar size and beginning at the first or second postanal myomere, are spaced uniformly (ca. 1 per myomere) along the ventral margin of the tail. Unlike preflexion-stage sargo, larval salema lack the melanophore embedded above the hindgut at the last preanal myomere, but as in sargo the number of melanophores along the ventral margin of the tail decreases to 10–19 (mode = 15) during notochord flexion and to 11–16 (mode = 13) in the postflexion stage. After the anal fin anlage begins to develop (ca. 4.3 mm), the first one or two melanophores (anterior to the anal fin base) usually move internally and disappear, and the next five to nine move ventrad onto the sides of the developing anal fin ray bases. The last melanophore along the anal fin base usually is embedded above the last ray base. During the early juvenile stage the melanophores along the peduncle move internally. At the end of the larval stage small melanophores develop along the anal fin rays (beginning as early as 15.5 mm). The amount of pigmentation is variable, from nearly absent to moderately heavy; when present, pigment is heaviest anteriorly between the first spine and fourth ray.

During the preflexion stage, 0–3 (mode = 1) small melanophores occur under the notochord tip; these become situated at the base(s) of any one (or more) of the four lowermost principal caudal rays (rarely, pigment is present at an upper caudal ray base, as well). At the end of the larval stage (ca. 15.5 mm) and during the early juvenile stage small melanophores develop along the sides of most principal caudal fin rays. This pigmentation tends to be densest along the middle rays, but a clear pattern (as in sargo) is absent.

Little or no pigment develops on the dorsal or lateral surfaces of the trunk and tail until the end of larval development (Fig. 14). The smallest specimen with dorsal trunk and tail pigment (15.5 mm) had this pigment in four areas: just anterior to the first dorsal spine (two pairs of melanophores), along each side of

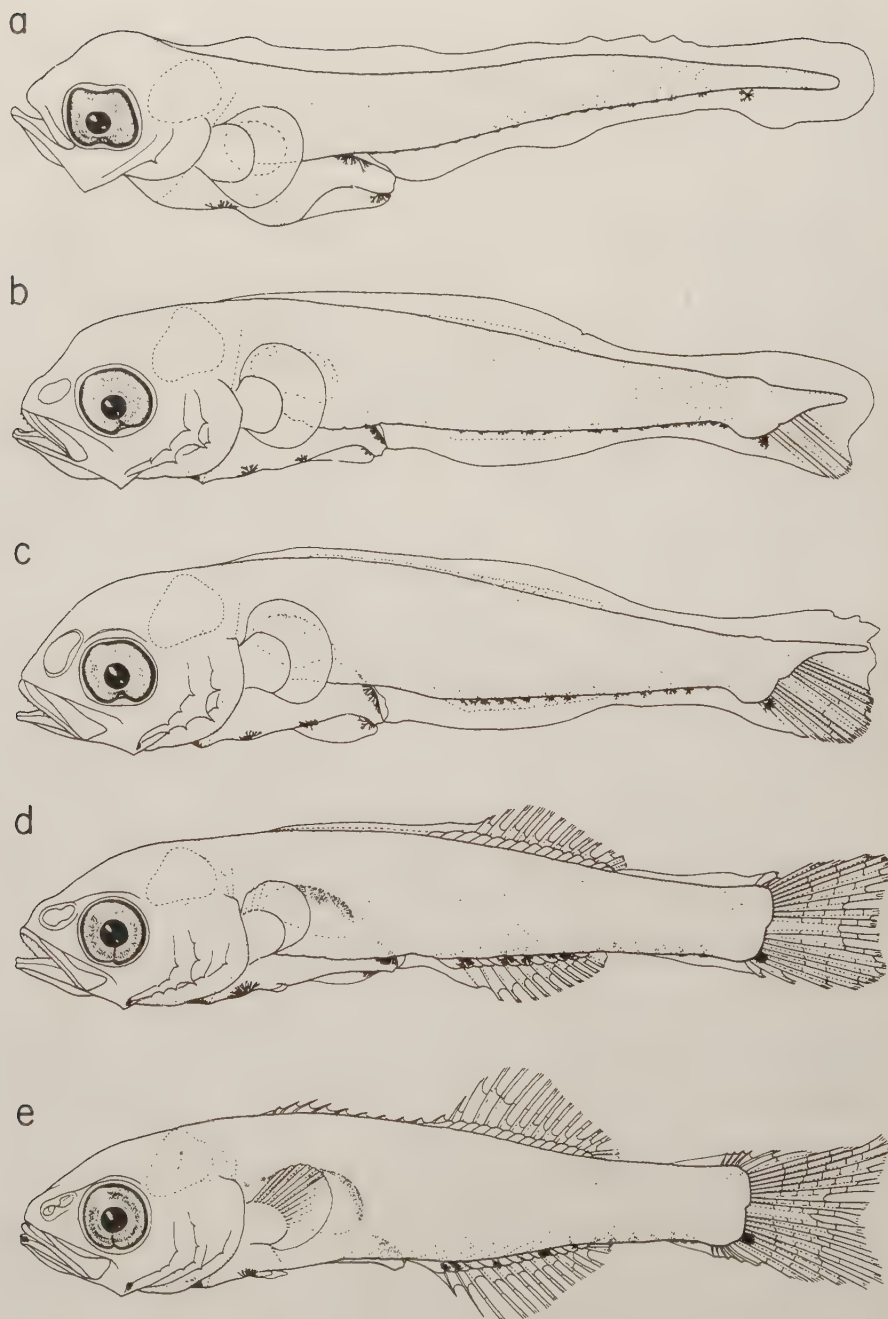


Figure 12. Larval salema, *Xenistius californiensis* (all SIO 91-135): a. 3.2 mm; b. 5.1 mm; c. 5.9 mm; d. 7.8 mm; e. 9.5 mm.

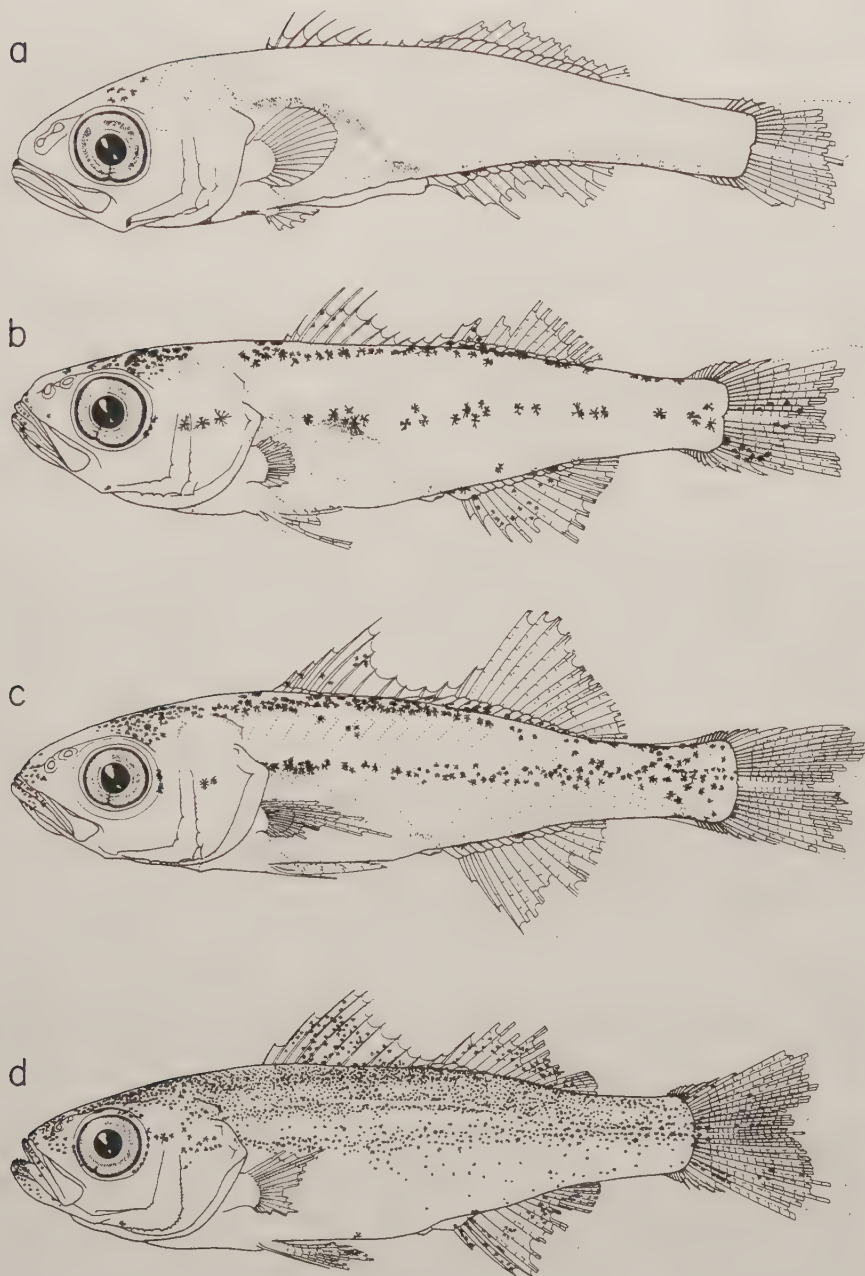


Figure 13. Larval (a), transforming (b, c), and juvenile (d) salema, *Xenistioides californiensis*: a. 12.9 mm (SIO 91-135); b. 15.5 mm (SIO 62-356); c. 20.6 mm (SIO 62-742); d. 32.2 mm (SIO 62-356).

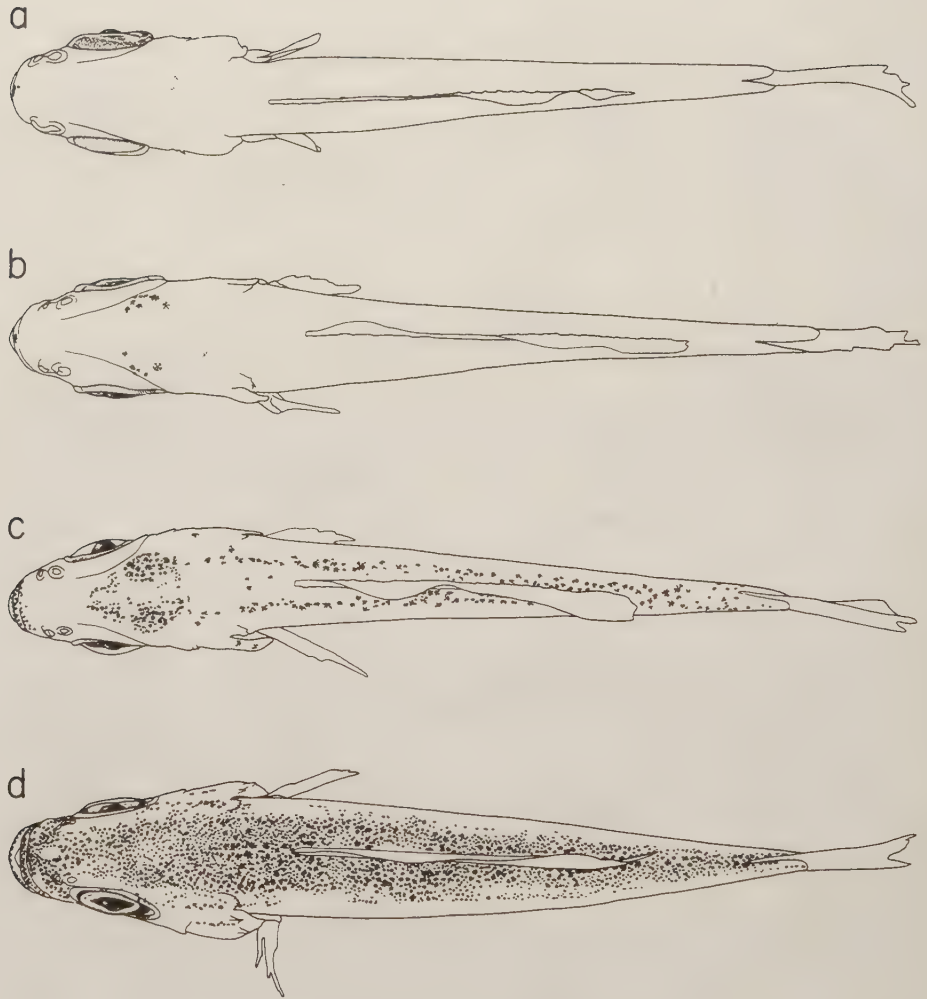


Figure 14. Larval (a, b), transforming (c), and juvenile (d) salema, *Xenistius californiensis*, in dorsal view: a. 9.5 mm (SIO 91-135); b. 12.9 mm (SIO 91-135); c. 20.6 mm (SIO 62-742); d. 32.2 mm (SIO 62-356).

the dorsal fin base from the fifth spine to the last ray (this pigment is continuous anteriorly with the dorsolateral diagonal band), midway along the caudal peduncle (five melanophores) and just anterior to the dorsal procurrent caudal fin rays (one melanophore). During the early juvenile stage dorsal melanophores fill in between these areas and scattered dorsolateral melanophores develop on the peduncle and below the dorsal fin (ca. 21 mm). Melanophores essentially cover the upper half of the body by ca. 32 mm; three longitudinal stripes (two are dorsolateral) are discernable at this size (Fig. 13d).

A few scattered melanophores develop on the membranes between the anterior six dorsal spines and anterior two rays at ca. 15.5 mm. Dorsal fin pigmentation is variable, but in juveniles larger than 21.8 mm it typically is heavy on the



Figure 15. Larval salemas, *Xenistius californiensis*, in ventral view (all SIO 91-135): a. 5.1 mm; b. 5.9 mm; c. 7.8 mm.

membranes between all the spines and along the outer half of the membranes between all rays.

Lateral trunk and tail pigment develops simultaneously with the dorsal trunk and tail pigment. The smallest specimen with lateral midline pigment (15.5 mm) had this pigment arranged in six patches (two to six melanophores in each patch) between the level of the swimbladder and the end of the peduncle. Melanophores quickly fill in between these patches (by ca. 20.6 mm) and the resulting band broadens, beginning posteriorly and progressing anteriorly. The dorsolateral and lateral pigment meet at the level of the soft dorsal fin by ca. 32 mm; at this size a few scattered (mostly myoseptal) ventrolateral melanophores are present.

The gut is always pigmented dorsally (internally) and ventrally (externally). However, anterior pigment, such as is seen in sargo, does not develop and external lateral pigment on the gut area is absent or nearly so until the end of the larval stage.

During the preflexion stage dorsal gut pigment (including swimbladder pigment) consists of one to three large melanophores covering the dorsal surface of the swimbladder (present in 97% of the specimens) and one (in 97%) or two (3%) large melanophores on the dorsal surface of the posterior hindgut. During the flexion stages the swimbladder pigment (always present) expands to cover its dorsal, dorsolateral and posterior surfaces. Swimbladder and hindgut pigment subsequently change little; an unpigmented area over the anterior hindgut nearly

always separates these (unpigmented area absent in only one of the 124 larvae examined). In about 5% of postflexion-stage specimens dorsal pigment develops on the gut, just anterior to the swimbladder.

Ventral pigment on the gut consists of one to six external melanophores along the ventral midline from the anterior midgut to the posterior hindgut. The number of melanophores decreases during larval development (Fig. 15), from a modal number of 3 (range 1–6) during the preflexion stage to 1 (range 0–4) during the postflexion stage, then to zero in juveniles (none visible by 21.8 mm). The first melanophore in this series is located at the pelvic fin base. The smaller melanophores along the posterior midgut and on the posterior hindgut typically persist only through the preflexion stage.

Lateral pigment on the abdominal area is absent through ca. 13 mm, remains sparse or absent until the lateral midline stripe develops, and typically is light up to the largest specimen examined (41.7 mm).

Head pigmentation during the preflexion stage usually is restricted to a melanophore on the ventral surface of the hindbrain (present in 90% of preflexion and all later specimens examined) and one on the isthmus just anterior to the cleithral symphysis (present in 68% of preflexion, and all later specimens). Near the end of notochord flexion (ca. 5.9 mm) a melanophore develops on each side of the posterior lateral surface of the midbrain (present in 11% of flexion and 89% of postflexion-stage specimens). An additional one or two posterior lateral midbrain melanophores may develop during the postflexion stage, although more commonly proliferation of this pigment does not begin until the end of larval development.

A few external dorsolateral melanophores develop on each side of the midbrain region beginning late in the postflexion stage (Fig. 14b). This pigment rapidly proliferates early in the juvenile stage to cover most of the dorsal and dorsolateral fore- and midbrain regions by ca. 21 mm (Fig. 14c), merging with the dorsal and dorsolateral trunk pigment by ca. 28 mm.

Melanophores first appear on the jaws during the postflexion stage (present in 10% of postflexion specimens smaller than 8 mm, and in 50% of those 8 mm or larger). During the larval stage this pigment consists of one or two melanophores at the premaxillary symphysis, occasionally with corresponding melanophores on the dentary (dentary pigment present in 25% of those larvae having upper jaw pigment). Pigment always is present across the anterior margins of both jaws during the juvenile stage, spreading upward across the snout and merging with the pigment over the brain by ca. 32 mm (Fig. 14d). The lower jaw pigment usually spreads downward and posteriorly onto the anterior gular membrane at the same time (gular pigment present in 5 of 7 juvenile specimens).

The only other head pigment during the larval stage is a melanophore at each angular. This may develop during the preflexion stage, as early as 3.8 mm, but more commonly is absent until ca. 5.1 mm (present in 12% of larvae 3.8–5.0 mm and in 90% of those larger than 5 mm).

During transformation to the juvenile stage (ca. 15.5 mm) pigment develops along the upper operculum, becoming continuous with the lateral midline stripe between ca. 21 and 28 mm. No other pigment develops on the head through the largest size examined (41.7 mm).

Morphology.—The smallest salema examined (2.2 mm) had no yolk or oil droplet. At this size the eye is pigmented, the mouth is functional, the swimbladder is inflated, and the gut is tubular and folded into a broad "S" shape. This fold tightens, forming a coil in the midgut between 3.8 and 4.0 mm. Notochord flexion begins at 4.3 mm and is completed between 5.9 and 6.2 mm. Transformation to

Table 4. Summary of measurements (in mm) of *Xenistius californiensis*. Body lengths are notochord length for preflexion and flexion-stage larvae, and standard length for postflexion and juvenile specimens. Measurements of body parts are summarized over 1 mm size classes; for each summary the mean measurement ($\bar{x}$), standard deviation (SD) and number of specimens measured (N) is given. Most specimens undergoing notochord flexion fall between the dashed lines below (the actual range of specimens undergoing notochord flexion is 4.3–6.2 mm); specimens below the dotted line are juveniles

Body length (mm)	Snout length			Eye diameter			Head length			Pre-Anus length			Pre-Dorsal fin length			Pre-Anal fin length			Body depth			Longest pre- opercular spine		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
2.0–2.9	0.1	0.03	8	0.3	0.02	9	0.6	0.1	9	1.1	0.1	9							0.5	0.1	9	0.02	0.02	9
3.0–3.9	0.2	0.04	17	0.3	0.03	17	0.9	0.1	17	1.5	0.2	17							0.7	0.1	17	0.1	0.03	17
4.0–4.9	0.3	0.1	13	0.4	0.03	13	1.2	0.1	13	2.0	0.2	13	2.1	0.3	2	2.5	0.4	5	1.0	0.1	13	0.1	0.02	13
5.0–5.9	0.5	0.1	13	0.5	0.1	13	1.6	0.2	13	2.6	0.2	13	2.3	0.4	13	3.0	0.2	13	1.2	0.1	13	0.1	0.02	13
6.0–6.9	0.6	0.03	17	0.6	0.04	17	2.0	0.1	17	3.3	0.2	17	2.5	0.5	15	3.6	0.2	17	1.5	0.1	17	0.1	0.03	17
7.0–7.9	0.6	0.1	28	0.7	0.1	27	2.2	0.2	28	3.8	0.2	28	3.0	0.7	28	4.1	0.2	28	1.6	0.1	28	0.1	0.02	28
8.0–8.9	0.8	0.1	16	0.8	0.1	16	2.6	0.1	16	4.4	0.2	16	3.1	0.4	15	4.7	0.2	16	1.8	0.1	16	0.1	0.02	16
9.0–9.9	0.8	0.04	8	0.9	0.1	8	2.9	0.2	8	4.9	0.2	8	3.2	0.1	8	5.1	0.2	8	2.0	0.1	8	0.1	0.02	8
10.0–10.9	0.8	0.03	2	0.9	0.1	2	2.9	0.3	2	4.9	0.6	2	3.2	0.3	2	5.1	0.6	2	2.0	0.2	2	0.1	0	2
13.0–13.9	1.2	—	1	1.4	—	1	4.5	—	1	7.9	—	1	5.4	—	1	8.1	—	1	3.1	—	1	0.1	—	1
15.0–15.9	1.4	—	1	1.6	—	1	5.4	—	1	9.2	—	1	5.8	—	1	9.4	—	1	3.8	—	1	0.1	—	1
21.0–21.9	1.9	0.3	2	2.1	0.1	2	7.4	0.6	2	13.1	0.1	2	7.8	0.2	2	13.1	0.1	2	5.8	0.1	2	0.1	0.04	2
28.0–28.9	2.4	—	1	2.8	—	1	9.6	—	1	12.5	—	1	10.7	—	1	12.5	—	1	7.8	—	1	0.1	—	1
29.0–29.9	2.3	—	1	2.9	—	1	9.8	—	1	17.2	—	1	10.3	—	1	17.2	—	1	7.8	—	1	0.1	—	1
30.0–30.9	2.3	—	1	3.1	—	1	10.2	—	1	18.2	—	1	10.8	—	1	18.2	—	1	8.5	—	1	0.1	—	1
32.0–32.9	2.8	—	1	3.0	—	1	10.8	—	1	19.4	—	1	11.1	—	1	19.4	—	1	8.8	—	1	0.1	—	1

the juvenile stage (indicated by scale formation, which is anterior to posterior) begins at ca. 15.5 mm and is complete by ca. 21 mm.

Larval development is a gradual process with no marked changes in body proportions (Figs. 12, 13; Table 4). Snout length, head length and pre-anus length all increase slightly relative to standard length during larval life. Snout length increases from an average 6% of standard length (range 3–7%) during the preflexion stage to 8% (range 6–10%) during notochord flexion and 9% (range 6–12%) in the postflexion and juvenile stages. Mean proportions (and ranges) for head length are: preflexion stage 25% (22–28%), flexion stage 29% (26–32%), postflexion stage 30% (27–35%), and juvenile 34% (33–36%). Respective values for pre-anus length are 44% (37–47%), 47% (44–53%), 52% (48–56%), and 57% (43–61%). Pre-dorsal fin length decreases as the fin develops, from a mean of 42% of standard length (range 32–53%) during notochord flexion to 39% (28–60%) in the postflexion stage and 36% (34–37%) in juveniles. Pre-anal fin length remains 55% (49–66%) of standard length throughout larval development. Similarly, body depth and eye diameter change little relative to standard length: depth averages 22% (15–26%) throughout larval life (but increases to 27%—range 26–28%—during the early juvenile stage), while eye diameter averages 10% (8–11%) through larval and early juvenile development.

Skeletal Development.—Alizarin staining of larval salema was less successful than the staining of sargo, and as a result, the sequence of developmental events was less fully determined. Nevertheless, from the material available, it appears that skeletal development differs little between the two species. Consequently, the description of skeletal development of salema is largely limited to Figures 16–22 and Tables 5–6; the narrative description consists of listings of differences from sargo, and limited supplemental information.

Neurocranium (Fig. 16, Table 5).—CHONDROCRANIUM. Development of the nasal septum is slightly later in sargo than in salema (ca. 4.2 mm vs. ca. 3.9 mm, respectively). The epiphysial cartilage is narrower and the anterior projection of the synotic tectum (prior to formation of the longitudinal cartilage between the synotic tectum and epiphysial cartilage) is smaller in salema than in sargo.

FRONTAL, PARIETAL. The parietal is somewhat narrower in salema than in sargo (Figs. 5, 16).

BASIOCCIPITAL, EXOCCIPITAL, SUPRAOCCIPITAL. The supraoccipital crest is smaller than that in sargo, and it does not acquire serrations along its dorsal margin (Figs. 5d, 16e).

BASISPHENOTIC, PARASPHENOTIC, PTEROSPHENOTIC, SPHENOTIC. There are no notable differences.

VOMER. The vomer begins to ossify at a slightly smaller size in salema (ca. 4.9 mm) than in sargo (ca. 6.5 mm), and apparently always lacks teeth. The vomer initially consists of two separate, slender ossifications: one forms on each side of the anterior margin of the ethmoid plate. These join mesially (5.5 mm) to form a slender crescent, just as in sargo.

EPIOTIC, PROOTIC, PTEROTIC. There are no notable differences.

LATERAL ETHMOID, MEDIAN ETHMOID. There are no notable differences.

NASAL. The nasals may begin to ossify slightly later in salema than in sargo (ca. 9.5 mm vs. ca. 8.5 mm, respectively).

CIRCUMORBITALS. The sequence of circumorbital ossification in salema could not be determined, except that the lacrymal is first, as in sargo. Development of the lacrymal begins earlier in salema than in sargo (ca. 5 mm vs. ca. 7 mm, respectively).

Table 5. Summary of skeletal development of *Xenistius californiensis*; size (mm SL) of smallest cleared and stained specimen with given structure visible as cartilage, or beginning to ossify; D = dermal origin

Structure	Size at first appearance of	
	Cartilage	Ossification
Neurocranium		
Basioccipital		3.9
Exoccipital		3.9
Parasphenotic		3.9
Pterosphenotic		7.4
Basisphenotic		21.2
Vomer		4.9
Lateral ethmoid		4.9
Median ethmoid		21.2
Lachrymal	D	4.9
Circumorbital 2	D	21.2
3	D	21.2
4	D	21.2
5	D	21.2
Dermosphenotic	D	21.2
Frontal	D	5.5
Parietal	D	6.8
Supraoccipital	D	4.9
Sphenotic		6.0
Pterotic		4.9
Prootic		4.9
Epiotic		6.0
Nasal	D	9.6
Jaws and suspensorium		
Premaxillary		3.9
Maxillary		2.7
Dentary		3.9
Articular	2.7	4.1
Angular	2.7	4.1
Hyomandibular	2.7	4.1
Symplectic	2.7	4.1
Quadrate	4.1	4.9
Ectopterygoid	4.1	5.9
Mesopterygoid		4.1
Metapterygoid	4.9	6.0
Palatine	5.8	6.0
Opercular series		
Preopercular	D	4.1
Opercular	D	4.1
Subopercular	D	4.9
Interopercular	D	4.9
Hyoid arch		
Branchiostegal	D	3.9
Ceratohyal	2.7	4.4
Epihyal	2.7	4.4
Interhyal	2.7	4.4
Ventral hypohyal	2.7	4.9
Dorsal hypohyal	2.7	6.0
Urohyal	D	4.9
Basihyal	4.9	7.4
Branchial arch		
Ceratobranchial	2.7	4.9
Epibranchial	4.4	4.9

Table 5. Continued

Structure	Size at first appearance of	
	Cartilage	Ossification
Hypobranchial	4.4	6.0
Basibranchial	4.4	6.0
Pharyngobranchial	4.4	7.4
Axial skeleton		
Vertebral centra		4.4
Urostyle		5.5
Neural arches	4.4	4.9
Haemal arches	4.4	5.9
Neural spines	4.4	9.6
Haemal spines	4.4	21.2
Epipleural ribs	D	9.6
Pleural ribs		9.6
Epurals	4.9	21.2
Hypurals 1-4	4.4	5.5
Hypural 5	6.3	9.6
Parhypural	4.4	5.5
Uroneurals	D	9.6
Caudal distal radials	9.6	
Dorsal pterygiophores	4.9	
Proximal radials	7.4	9.6
Distal radials	7.4	9.6
Anal pterygiophores	4.9	
Proximal radials	7.4	9.6
Distal radials	7.4	9.6
Pectoral and pelvic girdle		
Cleithrum		2.7
Supracleithrum	D	4.4
Dorsal postcleithrum	D	7.4
Ventral postcleithrum	D	4.9
Posttemporal	D	4.9
Supratemporals	D	21.2
Scapula	2.7	6.0
Coracoid	2.7	6.0
Pectoral proximal radials	4.9	21.2
Pectoral distal radials	21.2	
Basipterygia	7.4	21.2

Jaws and Suspensorium (Fig. 17, Table 5).—MAXILLARY, PREMAXILLARY, ROSTRAL CARTILAGE. The smallest cleared and stained specimen (2.7 mm) has a pair of long, slender, ossifying maxillaries, but apparently lacks premaxillaries. Small triangular premaxillaries are first visible at ca. 4 mm, and the rostral cartilage first appears at 4.5 mm.

ANGULAR, ARTICULAR, DENTARY. The lower jaw of the smallest cleared and stained specimen (2.7 mm) consists only of the slender Meckel's cartilages. Dentary ossification is first evident along the anterodorsal margin of each cartilage at ca. 4 mm. Dentary teeth apparently do not develop until ca. 4.5 mm, and form initially along the posterior half of each dentary instead of anteriorly, as in sargo.

HYOMANDIBULAR, SYMPLECTIC. There are no notable differences.

ECTOPTERYGOID, MESOPTERYGOID, METAPTERYGOID, PALATINE, QUADRATE. Ossification of the palato-ptyerygoquadrate cartilage may begin later in salemia than in sargo (Tables 2, 5).

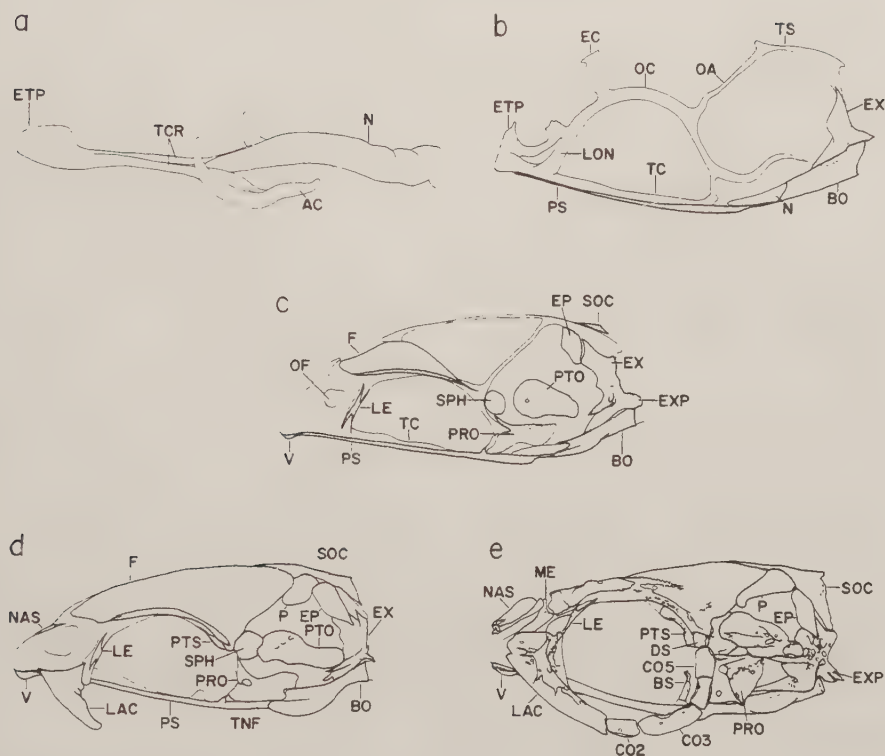


Figure 16. Lateral view of the developing neurocranium of salemia, *Xenistius californiensis*: a. 2.7 mm (SIO 91-135); b. 4.1 mm (SIO 91-135); c. 7.4 mm (SIO 91-135); d. 9.6 mm (SIO 91-135); e. 21.2 mm (SIO 62-356). White = cartilage; stippled = ossifying. Abbreviations are: AC = auditory capsule; TCR = trabecula cranii. All other abbreviations are defined in Figure 5.

Opercular Series (Fig. 17, Table 5).—Although the preoperculum and operculum were not visible until 4.1 mm in the cleared and stained salemia (Table 5), the first preopercular spine was clearly visible in an unstained 3.2 mm specimen (Fig. 12a), indicating that development begins at about the same size as in sargo (ca. 2.9 mm). The numbers of spines along the margins of the interior and exterior preopercular shelves differ little between the two species through at least 9.8 mm, but by ca. 21 mm salemia has about twice as many small spines along the margin of the interior (posterior) shelf (Figs. 6d, 17d). The uppermost opercular spine of salemia is distinctly larger than that of sargo (Figs. 6d, 17d).

The subopercular and interopercular were first visible at 4.9 mm, vs. 4.2 mm in sargo. Larval salemia develop only a single interopercular spine, compared with four or five in sargo.

Hyoid Arch (Fig. 18; Tables 5, 6).—Development of the bones of the hyoid arch apparently is slightly precocious in salemia, relative to development in sargo (Tables 2, 5).

Branchial Arches (Fig. 19; Tables 5, 6).—In contrast to the hyoid arch, development of the bones of the branchial arches may be slightly delayed in salemia, relative to development in sargo (Tables 2, 5). There are slight differences in the

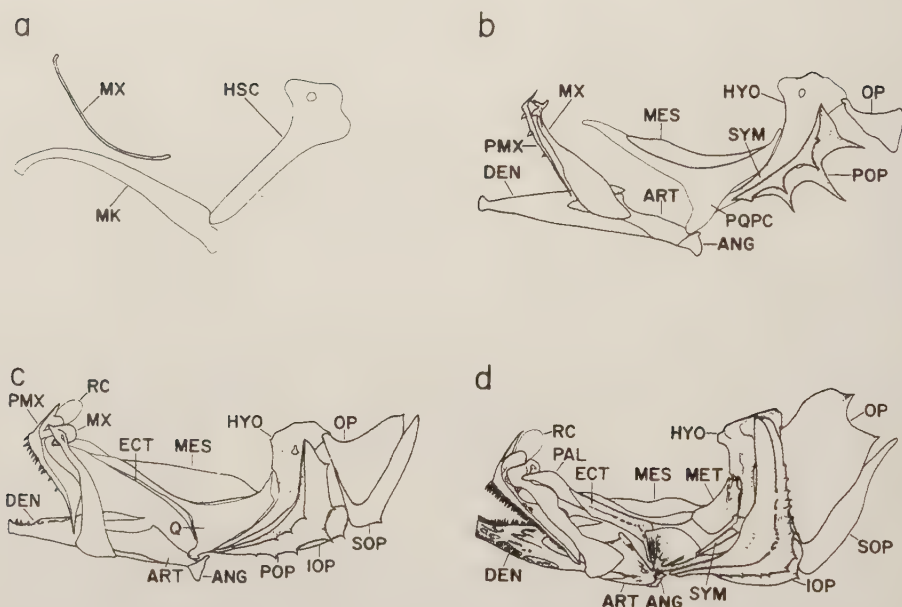


Figure 17. Development of the jaws, suspensorium, and opercular bones of salemia, *Xenistius californiensis*: a. 2.7 mm (SIO 91-135); b. 4.1 mm (SIO 91-135); c. 9.6 mm (SIO 91-135); d. 21.2 mm (SIO 62-356). White = cartilage; stippled = ossifying. Abbreviations are defined in Figure 6.

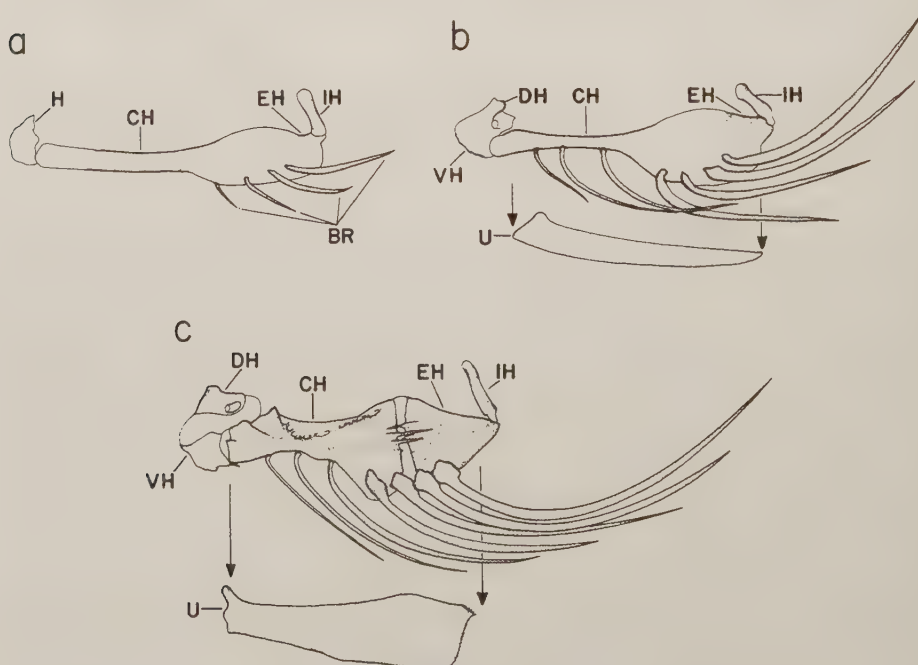


Figure 18. Development of the hyoid arch of salemia, *Xenistius californiensis*: a. 5.9 mm (SIO 91-135); b. 7.4 mm (SIO 91-135); c. 21.2 mm (SIO 62-356). White = cartilage; stippled = ossifying. Abbreviations are defined in Figure 7.

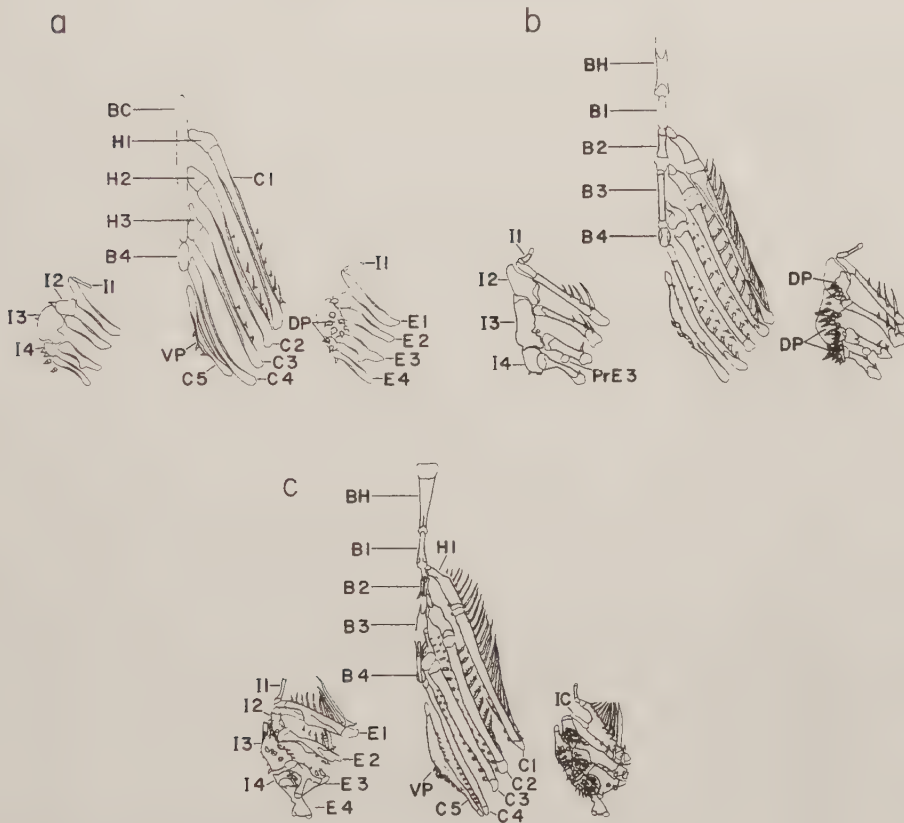


Figure 19. Development of the branchial arches of salemia, *Xenistius californiensis*: a. 6.0 mm (SIO 91-135); b. 9.6 mm (SIO 91-135); c. 21.2 mm (SIO 62-356). White = cartilage; stippled = ossifying. Abbreviations are defined in Figure 8.

sequence of ossification (e.g., basibranchial 4 begins ossifying before hypobranchial 3 in salemia, while the reverse is true for sargo), and salemia acquires more gill rakers than sargo (Tables 3, 6).

Axial Skeleton (Figs. 20, 21; Tables 5, 6).—**VERTEBRAL COLUMN** (Fig. 20). Development of the neural and haemal pre- and postzygapophyses could not be tracked in the cleared and stained salemia, since none were present in specimens 9.8 mm or smaller, but all were present in the next larger specimen (21.2 mm).

PLEURAL AND EPIPLEURAL RIBS. Salema acquires only 6–7 epipleural ribs, vs. 8–9 in sargo.

CAUDAL FIN (Fig. 21). Hypural 2 supports a single principal caudal ray through ca. 7 mm, but by ca. 9–10 mm the uppermost ray originally supported by hypural 1 shifts farther upward, to be supported jointly by hypurals 1 and 2. In comparison, hypural 2 of sargo originally supports two principal rays; the lowermost of these shifts downward to become jointly supported by hypurals 1 and 2. Like sargo, salemia has only two radial cartilages in the lower caudal skeleton, but in contrast to sargo, salemia has a small, separate radial cartilage adjacent to hypural 5 by 21.2 mm. Uroneural development could not be tracked in sargo; in salemia the

Table 6. Counts of fin spines and rays, vertebrae, ribs, gill rakers (outer arch: counts are given as epibranchial, and hypobranchial + ceratobranchial; one raker at the ceratobranchial-epibranchial articulation is counted with the ceratobranchial rakers), and branchiostegal rays in *Xenistius californiensis*. Specimens between dashed lines are undergoing notochord flexion; those below the solid lines are juveniles

Length (mm)	1°C	2°C	Fin rays					Ribs			Branchiostegal rays
			D	A	P ₁	P ₂	Vertebrae	Pleural	Epi-pleural	Gill rakers	
2.7											
3.9	3+3										5
4.1	2+2										4
4.2	5+5										4
4.3	3+3										6
4.4	3+3						2			0+2	5
4.4	4+4									0+3	6
4.9	7+6										
5.3	9+8						10+9			0+4	6
5.5	8+8						10+10			0+8	7
5.7	9+8						10+5			0+8	7
5.7*	9+8	0+1	12	10			10+14			0+7L,8R	7
5.8	9+8		3	3			10+5			1+9	7
5.9	9+8	0+1	7	5			10+7			0+7L,8R	7
6.0	7+7						10+2			0+8	7
6.0	9+8		9	8			10+7			0+6	6
6.3	9+8	0+1	11	11			10+12			0+7L,8R	7
6.3	9+8	0+1	10	10			10+12			0+9	7
6.5	9+8	0+1	I,13	I,12						0+10	7
6.8	9+8	0+2	—	11	2		10+16			1+13	7
7.4	9+8	1+1	II,12	I,12	4		10+14			1+10	7
7.8	9+8	2+3	IV+II,12	I,11	7	I,1	10+16			2+13	7
9.6	9+8	5+5	XII,12	II,12	13	I,5	10+16	4	3	4+16	7
21.2	9+8	13+12	XII,13	III,11	18	I,5	10+16	8	6	—	7
24.1	9+8	13+12	XI,14	II,12	I,17	I,5	10+16	8	7	12+26	7

* Postflexion specimen, probably shrunken.

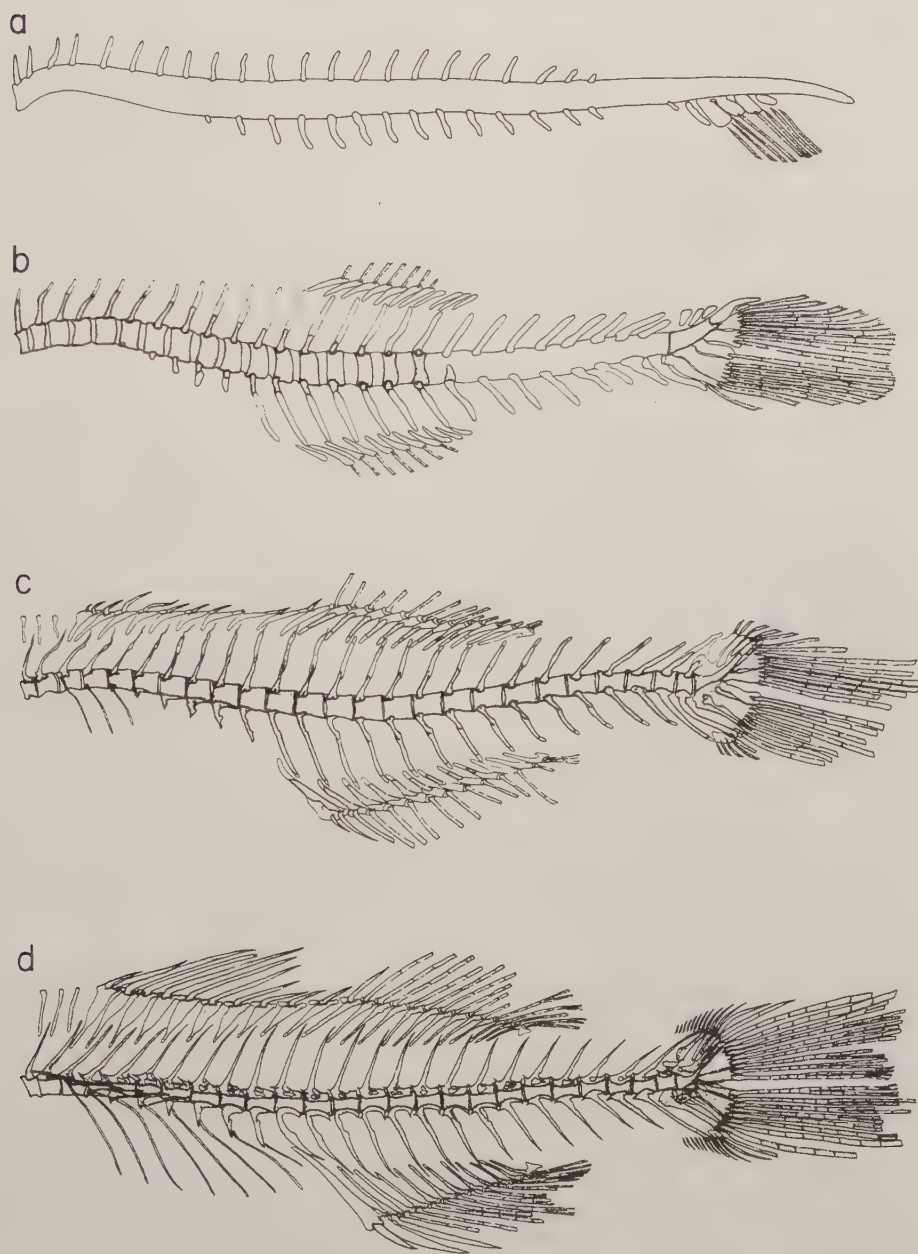


Figure 20. Development of the axial skeleton of salem, *Xenistius californiensis*: a. 4.4 mm (SIO 91-135); b. 5.9 mm (SIO 91-135); c. 9.6 mm (SIO 91-135); d. 21.2 mm (SIO 62-356). White = cartilage; stippled = ossifying.

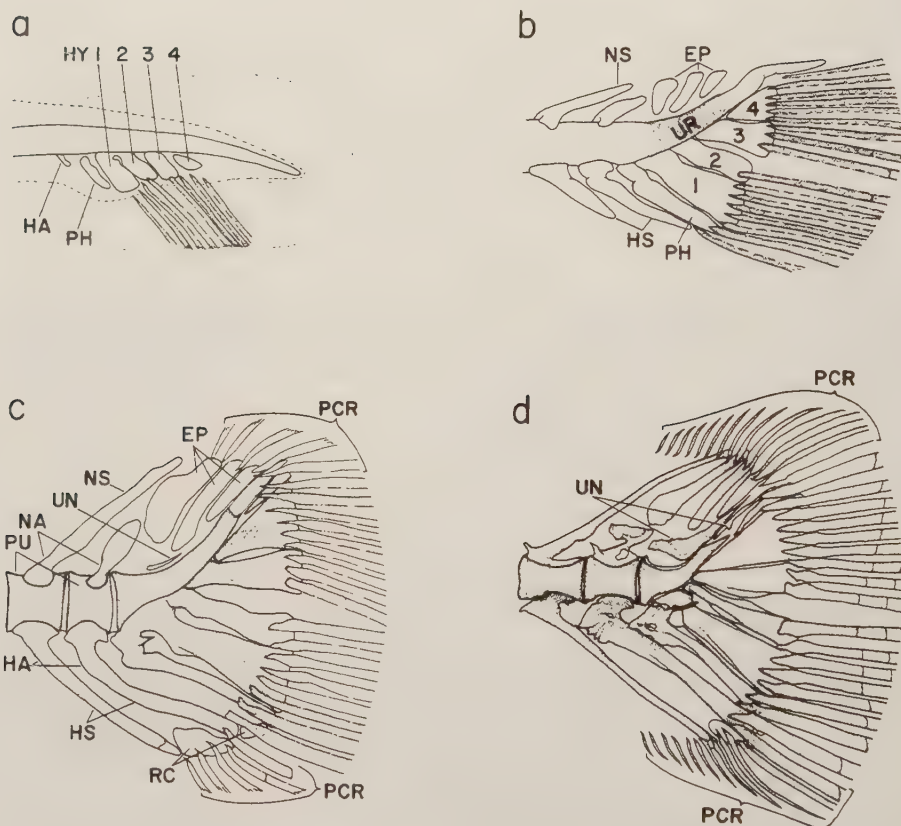


Figure 21. Development of the caudal skeleton of salemia, *Xenistius californiensis*: a. 4.4 mm (SIO 91-135); b. 5.9 mm (SIO 91-135); c. 9.6 mm (SIO 91-135); d. 21.2 mm (SIO 62-356). White = cartilage; stippled = ossifying. Abbreviations are defined in Figure 10.

anterior pair begins ossifying first, by 9.6 mm, and both pairs are well developed by 21.2 mm.

DORSAL AND ANAL FINS. Cartilaginous pterygiophores of the middle dorsal and anal fin rays are the first elements to form, at ca. 5 mm, with the rays following at ca. 5.5 mm (Tables 5, 6). It seems likely that the first anal pterygiophore (which supports the first two spines) results from the fusion of two cartilages: separate cartilages were not seen in any specimen, but in the 7.4 mm specimen a slender anterior section of cartilage is attached only at its proximal end to the remainder of the pterygiophore. The first dorsal pterygiophore (which supports the first two dorsal spines) does originate as two separate cartilages: both are visible and clearly separate in the 7.4 mm specimen. The second and third anal spines develop from rays, as in *Anisotremus virginicus* (Potthoff et al., 1984).

Pectoral and Pelvic Girdle (Fig. 22; Tables 5, 6).—The coracoscaphular cartilage is visible sooner, and the pectoral proximal radials may develop sooner, but ossify later, in salemia than in sargo (Tables 2, 5). The first cleavage of the cartilaginous pectoral blade was visible in a 4.4 mm specimen (it could not be determined

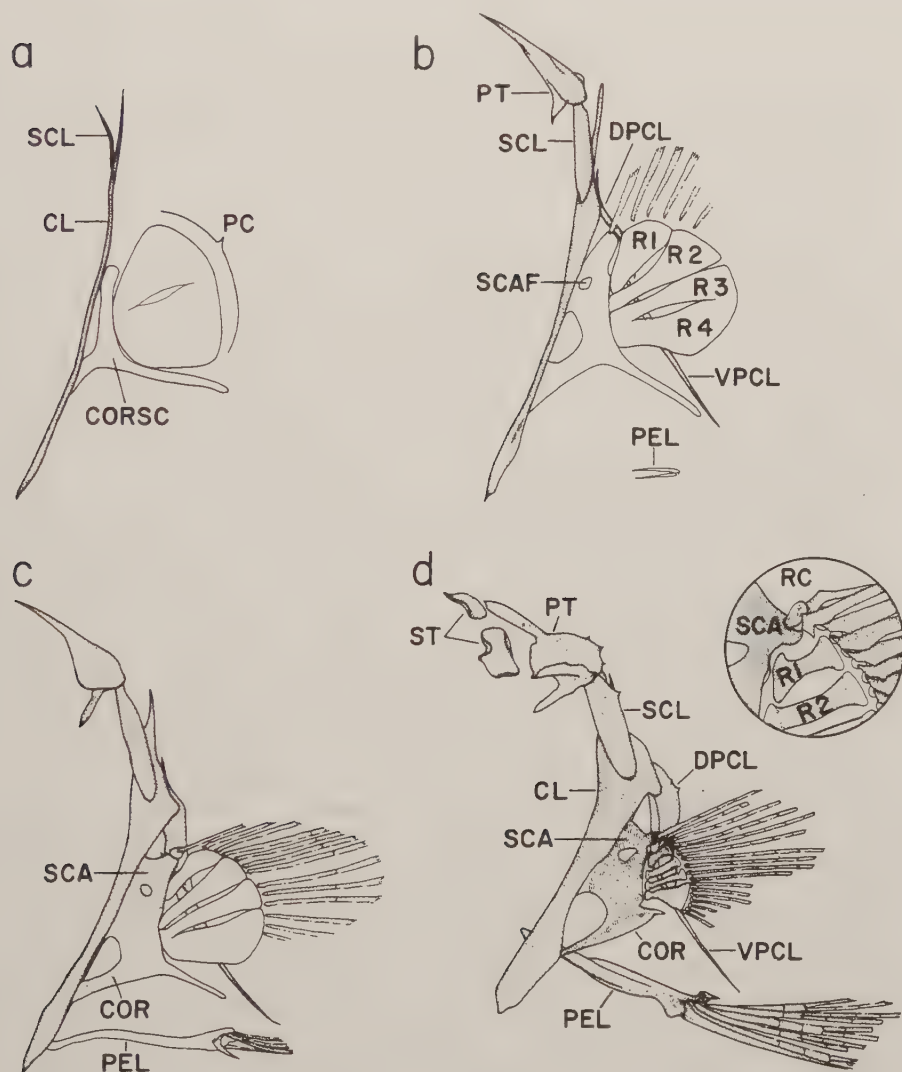


Figure 22. Development of the pectoral girdle of salema, *Xenistius californiensis*: a. 4.4 mm (SIO 91-135); b. 7.4 mm (SIO 91-135); c. 9.6 mm (SIO 91-135); d. 21.2 mm (SIO 62-356). White = cartilage; stippled = ossifying. Abbreviations are defined in Figure 11.

whether cleavages were present in any smaller specimen), and all three cleavages were visible by ca. 5 mm. It could not be determined when proximal radial ossification begins: none were ossifying through 9.6 mm, but all were ossifying in the 21.2 m specimen (Fig. 22).

IDENTIFICATION

Haemulid larvae resemble the lightly-pigmented larvae of many percoid families (Johnson, 1984; Leis and Rennis, 1983; Watson, 1983). However, in the

waters off California and northern Baja California, only larvae of the sciaenid, *Seriphus politus*, might be confused with larval sargo and salema. Confusion here can occur only for preflexion and early flexion-stage specimens; very small or damaged specimens cannot always be distinguished. Larval *S. politus* tend to be slightly deeper-bodied (depth 23–29% of SL) than sargo (19–28%) or salema (15–26%), and have a smaller eye (7–9% of SL, mean 8% during the preflexion stage, vs. 8–11%, mean 10% during the preflexion stage, for both sargo and salema). Pigmentation usually allows separation of the early larvae as well. The most reliable pigment character is the melanophore series along the ventral margin of the tail. Preflexion-stage sargo and salema both have series of evenly-spaced melanophores of approximately uniform size, while preflexion-stage *S. politus* have a series of approximately evenly-spaced and more-or-less uniform size melanophores along most of the tail, but much smaller, irregularly-spaced melanophores along the last 2–3 myomeres and under the notochord tip. The number of melanophores along the ventral margin of the tail subsequently decreases slightly in sargo and salema, but declines substantially in *S. politus* (usually <10 by mid-way through notochord flexion). Later, the higher dorsal and anal fin ray counts of *S. politus* allow easy and positive separation.

South of Bahia Sebastian Vizcaino, Baja California, positive identification of larval sargo and salema may be more difficult. In these waters, larval gerreids (*Eucinostomus* spp.), sparids (*Calamus brachysomus*), and several haemulid species might be confused with sargo and/or salema. Larval *C. brachysomus* are undescribed, but both they and larval *Eucinostomus* spp. should be separable from larval sargo and salema by myomere counts: the described sparid and gerreid larvae have 24 myomeres (rarely 25 in *Eucinostomus* spp.) vs. 26 (rarely 25) for sargo and salema. Larval *Eucinostomus* spp. also can be distinguished from sargo and salema by pigment characters and preopercular spines. *Eucinostomus* spp. develop external pigment (usually a pair of melanophores) over the midbrain at about the beginning of hypural development, while neither sargo nor salema acquire external pigment in this region until near the end of larval development. Throughout larval development the first 1–5 postanal myomeres (usually the first 2 or 3) are unpigmented in *Eucinostomus* spp.; during the preflexion stage (usually later, as well) both sargo and salema have pigment on all but the first one or two postanal myomeres. *Eucinostomus* spp. acquire dorsal pigment along the bases of the soft dorsal rays by ca. 7–8 mm while similar pigment first develops at a much larger size (>12 mm) in sargo and salema. Finally, *Eucinostomus* spp. have no, or at most very small (postflexion stage only), preopercular spines in contrast to the easily discernable preopercular spines of all but the smallest sargo and salema.

Larval development has not been described for any of the haemulid species that are sympatric with sargo and salema off southern Baja California and it is unknown how any of these, except *Orthopristis*, might be distinguished from larval sargo or salema. Larval *Orthopristis reddingi* have smaller, and fewer, spines on the opercular series bones and tend to have a longer preanal length than either sargo or salema (mean 53% of SL, vs. <50% for sargo and ≤52% for salema).

It can be difficult to distinguish larval sargo from salema prior to notochord flexion, but older specimens usually are easily separable. Many pigment and morphometric characters differ somewhat between the two species, but do not reliably distinguish individual specimens during the preflexion stage. However, two pigment characters do consistently differ between sargo and salema: sargo usually have pigment on the peritoneum just anterior to the liver (present in 87% of preflexion sargo, absent in preflexion salema), while salema nearly always have

a melanophore under the anterior hindbrain (present in 90% of salema, and in 4% of preflexion sargo). The presence or absence of anterior peritoneal pigment usually allows species identification through notochord flexion; during this stage sargo becomes noticeably deeper-bodied as well (mean depth 25% of SL vs. 23% for salema). Morphometric differences (body depth, pre-anus length), pigmentation (especially the midbrain pigment of salema), and dorsal soft ray counts (14–15 for sargo, 12–13 for salema) allow easy separation of postflexion-stage specimens.

DISCUSSION

The purpose of this discussion is to briefly compare the larval development of sargo and salema with development in other haemulids. Larvae of the two haemulid subfamilies, Haemulinae and Plectorhynchinae, apparently differ both in pigmentation and morphology. Haemulines are lightly pigmented through most of the larval stage, but develop a pattern of two or more longitudinal stripes along the upper half of the body early in the juvenile stage (Courtenay, 1961; Hong, 1977; Leis and Rennis, 1983; Lindeman, 1986; Potthoff et al., 1984; Saksena and Richards, 1975; Watson, 1983). Plectorhynchines also are relatively lightly pigmented early in larval development, but may become moderately to heavily pigmented subsequently (Kobayashi and Iwamoto, 1984; Leis and Rennis, 1983); *Parapristipoma* is an exception in that it remains lightly pigmented (Okiyama, 1988), like the haemulines.

Larval haemulines are relatively slender (Leis and Rennis, 1983; Lindeman, 1986; Potthoff et al., 1984; Saksena and Richards, 1975; Watson, 1983), while larval plectorhynchines, except *Parapristipoma*, tend to be somewhat deeper-bodied (Leis and Rennis, 1983; Kobayashi and Iwamoto, 1984; Okiyama, 1988). Larval sargo and salema are typical haemulines both in pigmentation and morphology, except that sargo, as well as *Anisotremus virginicus* (Potthoff et al., 1984), is somewhat deeper-bodied than the other described haemulines.

The few published descriptions of skeletal development in Haemulidae that are available for comparison with development in sargo and salema are of haemulines: Potthoff et al. (1984) described development of *Anisotremus virginicus*, Lindeman (1986) described development of *Haemulon flavolineatum* from ca. 6 mm, and Saksena and Richards (1975) described ossification in *H. plumieri*. In addition to these descriptions, seven cleared and alizarin-stained *Orthopristis chrysoptera* (3.4–13.0 mm: preflexion through late postflexion) were examined in the present study.

Based on these few species, it appears that skeletal development differs little among the Haemulinae; differences between species are largely limited to small differences in the size at which developmental events occur (Table 7), small differences in the shapes of some bones, and differences in the number of elements in some skeletal structures (Table 8). Very few consistent intergeneric differences are discernable, although it appears that there may be gradients in larval size at onset of ossification, and in the number and size of spines on the opercular series bones and pectoral girdle.

Although the order in which bones ossify differs little among the Haemulinae, ossification of most bones begins at a somewhat smaller larval size in *Anisotremus* and *Xenistius* than in *Orthopristis*, which in turn may begin ossifying at a slightly smaller size than *Haemulon* (Table 7). Ossification in *Anisotremus* may be slightly precocious relative to that in *Xenistius*.

Orthopristis apparently has the smallest, and least numerous spines on the opercular bone series among the Haemulinae (Table 8; Lindeman, 1986). *Xenistius*

Table 7. Larval size at the beginning of ossification of selected skeletal elements in Haemulinae. Sources of information are: *Anisotremus davidsonii* (this study), *A. virginicus* (Potthoff et al., 1984), *Haemulon flavolineatum* (Lindeman, 1986), *H. plumieri* (Saksena and Richards, 1975), *Orthopristis chrysoptera* (this study), *Xenistius californiensis* (this study)

Structure	Approximate size at beginning of ossification (mm)					
	<i>Anisotremus davidsonii</i>	<i>A. virginicus</i>	<i>Haemulon flavolineatum</i>	<i>H. plumieri</i>	<i>Orthopristis chrysoptera</i>	<i>Xenistius californiensis</i>
Neurocranium						
Frontal	5	—	11–13	≤10	7	5.5
Parietal	6.6	—	11–13	≤10	7	7
Supraoccipital crest	8.5–9	—	19–20	≤10	12	7–7.5
Vomer	6.6	—	—	4.6	6.3	5
Jaws and suspensorium						
Dentary	≤2.9	—	≤6.2	4.6	≤3.4	3.9
Premaxillary	≤2.9	—	≤6.2	5.8	≤3.4	3.9
Quadrate	4.2	—	≤6.2	4.6	5.1	4.9
Symplectic	3.9	—	>6.2, ≤9–10	4.6	5.1	4.4
Opercular bones						
Interopercular	4.2	5.7	≤6.2	5.8	6.3	4.9
Opercular	≤2.9	5.7	≤6.2	8.2	5.1	4.4
Preopercular	≤2.9	3.5	≤6.2	4.6	5.1	4.4
Subopercular	4.2	5.7	≤6.2	5.8	6.3	4.9
Hyoid arch						
Branchiostegal	3.9	3.5	≤6.2	4.6	≤3.4	3.9
Ceratohyal	3.9	7.5	≤6.2	5.8	5.1	4.4
Epihyal	4.2	7.5	≤6.2	5.8	5.1	4.4
Hypohyal	4.6–5.7	7.5–10	—	5.8	7	4.9–6
Branchial arch						
Basibranchial	5.5	5.7	>6.2	5.8	7	6
Ceratobranchial	4.2	5.7	>6.2	5.8	6.3	4.9
Epibranchial	4.2	5.7	>6.2	5.8	6.3	4.9
Gill rakers	4.3	3.8	≤6.3	5.8	6.3	4.3
Hypobranchial	5.5	5.7	>6.2	5.8	≤12	6
Axial skeleton						
Vertebral centra	4.5	>4.3, ≤5.7	8.5–9	9.2	6.3	4.4

has more preopercular spines than *Anisotremus* or *Haemulon*, but fewer interopercular spines than *Anisotremus* (Table 8). All of these spines are about the same size as the corresponding spines in *Anisotremus* and *Haemulon*. In addition to the opercular series spines, *Anisotremus* and *Xenistius* acquire one or two small supracleithral spines and about three small posttemporal spines. These are lacking in *Orthopristis*, and it is unclear whether *Haemulon* has them or not. *Pomadasys* is distinctly spinier, with several small to moderate spines each on the preopercular margins and on the interopercular and/or subopercular margins, moderate supracleithral and/or posttemporal spines, and small supraocular spines (Leis and Rennis, 1983). *Conodon* is highly ornamented, with several moderate to large preopercular spines, interopercular and/or subopercular spines, supraocular and other head spines, and apparently with cleithral spines in addition to supracleithral and posttemporal spines (Heemstra, 1974; Johnson, 1984). The described plectorhynchines fall between *Pomadasys* and *Conodon* in this series, except *Parapristipoma*, which is more like *Anisotremus* and *Xenistius* (Kobayashi and Iwamoto, 1984; Leis and Rennis, 1983; Okiyama, 1988).

Table 8. Counts of selected skeletal elements acquired in larvae or young juveniles of Haemulinae. Gill raker counts refer to the outer arch, and are given as hypobranchial + ceratobranchial, and epibranchial rakers. The number of caudal distal radial cartilages refers to the number in the ventral caudal skeleton. Sources of information are: *Anisotremus davidsonii* (this study), *A. virginicus* (Poitthoff et al., 1984), *Haemulon flavolineatum* (Lindeman, 1986), *H. plumieri* (Sakana and Richards, 1975), *Orthopristis chrysoptera* (this study), *Xenistius californiensis* (this study)

Structure	Counts					
	<i>Anisotremus davidsonii</i>	<i>A. virginicus</i>	<i>Haemulon flavolineatum</i>	<i>H. plumieri</i>	<i>Orthopristis chrysoptera</i>	<i>Xenistius californiensis</i>
Gillrakers	13-16 + 9-12	14-16 + 7-11	13-15 + 9-10	15 + 10	12 + 4-5	26 + 12
Interopercular spines	4-5	2-4	—	1-2	0	1
Preopercular spines						
Interior shelf	7-8	10-12	ca. 7-9	ca. 5-10	4-5	14-15
Exterior shelf	2-3	2-3	ca. 4	ca. 3	0-3	3-4
Subopercular spines	1	1-3	—	1-2	0	1
Vertebrae	10 + 16	10 + 16	10 + 16	10 + 15-16	10 + 16	10 + 16
Pleural ribs	8	8	8	—	8	8
Epipleural ribs	8-9	11-12	11	> 10	≥ 6	6-7
Dorsal fin rays	XI, 14-15	XII-XIII, 15-16	X-XII, 14-15	XII, 15-16	XII, 15-17	XI-XII, 12-14
Anal fin rays	III, 9-10	II, 11-12 (III, 10-11)	II, 9(III, 8)	II, 10 (III, 9)	II, 14-15 (III, 13-14)	II-III, 11-12 (III, 11-12)
Pectoral fin rays	17-19	16-17	14-16	16-17	17-19	17-18
Procurent caudal rays	12-14 + 11-13	13 + 12	10-12 + 11-12	10-12 + 10-12	13 + 12	13 + 12
Caudal distal radial cartilages	2	3	2	—	2	2

Vomerine teeth are present in larval *Anisotremus davidsonii* and *Orthopristis chrysoptera*, but absent in *Xenistius californiensis*. The presence or absence of vomerine teeth was not noted in the studies of other species. Most haemulids lack vomerine teeth as adults (Johnson, 1980) and their presence in larvae might prove useful in examining relationships, once more is known of their occurrence in the various haemulid genera. Furthermore, the existence of gradients in the size at initiation of ossification and in the degree of head and pectoral girdle spination might also prove of value in examining phylogenetic relationships among the haemulid genera. However, the potential utility of these characters cannot be assessed until larval development within the family is much more fully documented.

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Oxygen- and Nitrogen-Dependent Sulfur Metabolism in the Thiotrophic Clam *Solemya reidi*

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Abstract. We investigated aerobic and anaerobic thiotrophic metabolism by the gutless clam *Solemya reidi* and its intracellular symbiotic bacteria. Mean environmental sulfide concentrations in porewater next to animals varied from a high of 888 μM to a low of 17 μM in different sediment samples, while mean thiosulfate concentrations were very low (1–13 μM). The blood of freshly collected clams contained up to 300 μM thiosulfate but little sulfide ($\leq 12 \mu\text{M}$). In experimental incubations, clams were able to take up thiosulfate, yet under no conditions could the animals concentrate thiosulfate above external concentrations. Thiosulfate accumulation in the blood during incubations was the result of aerobic but not anaerobic sulfide oxidation by the animals. This finding and previous observations of the presence of high concentrations of thiosulfate in the blood of field-caught clams indicate that the animal portion of the symbiosis normally functions aerobically. The intact symbiosis exhibited nitrate and nitrite respiration under anoxic conditions. Nitrate respiration was stimulated by sulfide, as well as thiosulfate, while nitrite respiration was only stimulated by sulfide. Nitrate respiration also occurred when whole animals were under oxic conditions. Respiration measurements showed that the bacterial symbionts were capable of direct sulfide oxidation. Sulfide-stimulated oxygen consumption by bacterial preparations from the gills of mud-maintained clams reached a maximum rate at 25 μM sulfide and showed no apparent inhibition at sulfide concentrations up to 1 mM sulfide.

Introduction

Solemya reidi is a gutless, marine protobranch bivalve that lives in reduced sediments such as sewage outfall

zones and pulp mill effluent sites (Reid, 1980; Reid and Bernard, 1980). The clam contains intracellular, chemolithotrophic bacterial symbionts within specialized cells in its gills (Felbeck, 1983). The bacteria use the energy from the oxidation of reduced sulfur compounds to fix and reduce CO_2 and subsequently translocate the fixed carbon to symbiont-free tissues of the animal, resulting in a net autotrophic existence of the symbiosis (Felbeck, 1983; Fisher and Childress, 1986; Anderson *et al.*, 1987). This autotrophic, sulfur-dependent mode of nutrition is called thiotrophy (Vetter, 1991).

Based on experiments done at high sulfide concentrations, Powell and Somero (1985) concluded that sulfide oxidation occurs in the animal tissue of *S. reidi* and not in the symbiotic bacteria. The authors identified intracellular, ferric iron-containing granules (originally called sulfide-oxidizing bodies, referred to as granules in this manuscript) and based upon a colorimetric assay suggested that granules were responsible for sulfide oxidation in *S. reidi* (Powell and Somero, 1985). The products of this oxidation were not identified. Subsequent studies revealed that isolated mitochondria of *S. reidi* are also capable of sulfide oxidation and that the mitochondria couple sulfide oxidation to aerobic respiration and ATP production (Powell and Somero, 1986; O'Brien and Vetter, 1990). The mitochondria oxidize sulfide exclusively to thiosulfate (O'Brien and Vetter, 1990). In addition, high concentrations of thiosulfate are found in the blood of field-caught animals and clams experimentally exposed to sulfide (Anderson *et al.*, 1987). These findings suggested that the mitochondria may also have a role in sulfide detoxification.

Current models propose that the detoxification of sulfide is an oxygen-dependent process that occurs only in the animal tissues of *S. reidi* (reviewed by Somero *et al.*, 1989). The oxidation results in the production of thio-

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sulfate. Thiosulfate is subsequently transported by the animal to the bacteriocyte where it is further oxidized by the bacteria, again by an oxygen-dependent respiratory process.

Aspects of this model describing thiotrophic metabolism are not proven or they are inaccurate because of a lack of direct experimental evidence or the technical difficulties in early experiments. First, there is little information on the environmental sulfide conditions in the clam's habitat. Although the bulk sulfide concentrations in sediment samples are highly variable, ranging from low micromolar concentrations up to 22 mM (Childress and Lowell, 1982; Vetter *et al.*, 1989), the concentration near the animals is not known. Data suggest that the optimal sulfide concentrations for the animals are 100 μ M or below (Anderson *et al.*, 1987, 1990). In addition, the concentrations of other possible substrates (including thiosulfate, which is found in the blood of freshly caught clams) in the animals' burrows are not known.

Second, bacterial symbionts may be important agents of direct sulfide oxidation in the symbiosis in the presence of environmental sulfide concentrations. Recent experiments in our laboratory have shown that enriched bacterial suspensions show stimulation of $^{14}\text{CO}_2$ uptake in the presence of 500 μ M sulfide and exhibit nitrate and nitrite respiration under anoxic conditions in the presence of 200 μ M sulfide (Dr. Barbara Javor, pers. comm.). In addition, *in vivo* measurements of spectral changes of intracellular hemoglobins (Doeller *et al.*, 1988) and *in vitro* accumulations of elemental sulfur in isolated gill ctenidia exposed to oxygen and sulfide (Vetter, 1990) suggest that sulfide and oxygen enter the bacteriocyte directly from the seawater.

Third, the effect of anoxic conditions on sulfur metabolism of the host and symbionts needs additional study. Anderson *et al.* (1990) have shown that animal tissues of *S. reidi* maintain aerobic metabolism in the presence of sulfide concentrations up to 100 μ M, but they switch to anaerobic metabolism (fermentation) in the presence of oxygen at higher sulfide concentrations. This switch is due to poisoning of cytochrome *c* oxidase and aerobic respiration (Anderson *et al.*, 1990). Whole animal experiments under conditions of low O_2 or at sulfide concentrations above 250 μ M showed a loss of net autotrophy, suggesting that bacterial metabolism was inhibited (Anderson *et al.*, 1987). However, the anaerobic sulfide-oxidizing capacity of the symbionts was never measured and the clams were incubated in surface seawater that does not typically contain the alternate electron acceptor nitrate that some sulfur-oxidizing bacteria can use for anaerobic respiration. Thus, the absence of net autotrophy observed could be due to the absence of nitrate. Net CO_2 uptake might be enhanced at high sulfide concentrations or at

low O_2 concentrations under conditions promoting anaerobic respiration in the bacteria.

High nitrate reductase activity has been observed in *S. reidi* (Felbeck *et al.*, 1983). However, this enzyme was proposed to be involved only in assimilatory nitrate reduction. The bacterial symbionts of the clam *Lucinoma aequizonata* might use an anaerobic metabolic strategy (Cary *et al.*, 1989), and recently nitrate respiration has been demonstrated in the symbionts of *L. aequizonata* (U. Hentschel, pers. comm.) and *S. reidi* (Javor, pers. comm.). The sulfur metabolism of the whole clam under oxic and anoxic conditions in the presence of nitrate needs to be investigated.

This investigation was designed to address the following questions about sulfide and thiosulfate metabolism in the *S. reidi* symbiosis. (1) Is thiosulfate present in the mud around the clam and what causes thiosulfate to accumulate in clam blood? (2) Can the bacteria oxidize sulfide directly, and do bacteria and granules compete for sulfide? (3) Can the intact symbiosis use nitrate and nitrite as alternate electron acceptors?

Materials and Methods

Experimental animals

Specimens of *Solemya reidi* were collected at the Hyperion sewage outfall in Santa Monica Bay, California, at a depth of 100 to 140 m using a modified Van Veen grab. The animals were maintained in mud from their habitat in a flowing seawater aquarium. The aquarium was kept dark at 8°C to mimic natural conditions. All experimental incubations were done with animals maintained less than 30 days, with most animals maintained less than 14 days. Clam size varied from 32 to 42 mm. An effort was made to use similar size animals within experiments. Nitrate and nitrite respiration experiments (Figs. 1, 2) have all values normalized to a wet gill weight of 420 mg/clam. Blood values (Tables I, II, III) are not normalized to size or gill weight. The values represent the concentrations measured.

Whole clam sulfur use experiments (oxic and anoxic) were done with aquarium-maintained animals that had been pre-incubated for a minimum of 48 h in oxygenated seawater (dark at 8°C) without sulfur substrates. This pre-incubation allowed the animals to remove reduced sulfur compounds from their blood (see Results). All incubations were performed in a glass, water-jacketed incubation chamber with 500 ml of filtered seawater at 10°C. Whole clam nitrate and nitrite respiration experiments were done with aquarium-maintained animals immediately after removal from the mud. Incubations were done in ground-glass stoppered bottles with 100 ml filtered seawater at 10°C. All anoxic incubations were done in seawater sparged with argon for 10 min. The chambers were sealed

except for sampling, and argon was blown over the opening during sampling.

Sulfur compound sampling and analysis

Concentrations of sulfide, thiosulfate, sulfite, and glutathione were measured by HPLC using the monobromobimane (bimane) technique (Newton and Fahey, 1987; Vetter *et al.*, 1989). For porewater samples, the sediment surrounding individual animals was collected and immediately placed in 50-ml test tubes and centrifuged in a clinical centrifuge at approximately 2500 RPM. Aliquots of 100 μ l were immediately derivatized with bimane. The reaction of bimane with the sample rapidly derivatized all reduced thiols and prevented further oxidation. Blood samples were collected by carefully cutting the membrane that connects the two valves and opening the animal. Seawater was wiped away, and the mantle was cut at the exhalant opening. Aliquots of 100 μ l blood were immediately derivatized with bimane. Water samples from whole animal incubations were collected and 100 μ l aliquots were immediately derivatized with bimane. Fluorescence of the bimane-derivatized samples was measured as previously described (Wilmot and Vetter, 1990).

Bacterial enrichments

Suspensions of bacterial symbionts were obtained by gently homogenizing the gills of aquarium-maintained clams in a glass homogenizer in filtered (0.45 μ M) seawater buffered with 10 mM MOPS (3-[N-morpholino]propanesulfonic acid), pH 7.5. The homogenate was centrifuged at low speed ($53 \times g$) at 4°C for 5 min, pelleting the large cellular debris. Filtration of the suspension through 15- μ m or 28- μ m Nitex filters separated the bacteria (approximately 1 μ m diameter) from the larger subcellular particles. The filtrate was centrifuged a second time at $1925 \times g$ at 4°C for 5 min, which pelleted the bacteria and granules while leaving the mitochondria in the supernatant. The pellet was washed and resuspended in MOPS-buffered seawater. The Percoll gradient technique (Distel and Felbeck, 1988; Wilmot and Vetter, 1990) was not effective in separating the bacteria from other subcellular particles. Light microscopy was used to confirm that preparations did not contain nuclei and large cellular debris. Because mitochondria are too small to detect by casual observation, the bacterial preparation was tested for contamination by measuring ATP production. There was no external ATP produced, indicating that either no mitochondria were present or they could not function in seawater. Bacterial preparations had a final concentration of 36–38 mg wet gill tissue/ml seawater.

Bacterial enrichments were also made from clams that had been starved for 21 days. These animals were placed in oxygenated seawater containing no sulfur substrates or

nitrate and kept at 8°C in the dark. The seawater was changed at least once a day. The bacterial suspensions were prepared exactly as described above.

Protein determination

Total protein of bacterial suspensions was measured by the method of Hartree (1972).

Nitrite determination

Seawater samples (1 ml) were collected and nitrite determined using a modification of the colorimetric method of Strickland and Parsons (1977). Due to interference by thiols, several modifications were necessary. Briefly, we had to solve the problem of interference by sulfide and thiosulfate. This was accomplished by precipitating the thiols.

Respiration measurements

All incubations were carried out in a Strathkelvin respiration chamber at 15°C. The respiration chamber was thermally jacketed and contained a stir bar that allowed homogeneous incubation at a constant temperature. Oxygen consumption was measured with a Clark-type oxygen electrode (Strathkelvin Instruments) modified to reduce interference by H₂S (O'Brien and Vetter, 1990).

Results

Sediment porewater and blood sulfur compounds

To determine which reduced sulfur compounds were available to the clams, we sampled the sediment porewater surrounding individual clams and in the blood of these clams. The major sulfur compound in sediment porewater was sulfide (Table I). Extremely low concentrations of thiosulfate were measured, but no sulfite or glutathione was present. Mean sulfide concentrations were highly variable between sediment samples at different sites (ranging from a low of 17 μ M to a high of 888 μ M). Variability within sediment samples was considerably less.

Although sulfide was the major reduced sulfur compound in the seawater surrounding the animals and thiosulfate concentrations were extremely low, clam blood contained high concentrations of thiosulfate (Table I). The blood of the animals also contained low concentrations of sulfide and sulfite ($\leq 12 \mu$ M). The cellular thiol compound, glutathione, remained relatively constant throughout sampling and was used as an indicator that hemolymph samples were not diluted by seawater. Nitrite was not present in either the sediment porewater or blood from freshly collected animals (data not shown).

To determine how fast thiosulfate and sulfide could be cleared from the blood of freshly collected animals from

Table I

Sulfur compounds from sediment porewater and blood of freshly collected *Solemya reidi*

Sample	n	Sulfur compounds (μM)			
		Sulfide	Thiosulfate	Sulfite	Glutathione
Pore water					
May 1987	6	385 $\pm$ 321	11 $\pm$ 19	ND	ND
June 1987	6	17 $\pm$ 5	1 $\pm$ 0	ND	ND
July 1990	6	38 $\pm$ 30	13 $\pm$ 2	0	0
September 1990 #1	4	20 $\pm$ 8	3 $\pm$ 1	0	0
September 1990 #2	6	888 $\pm$ 60	5 $\pm$ 4	0	0
Blood					
May 1987	6	4 $\pm$ 11	297 $\pm$ 120	ND	ND
June 1987	6	1 $\pm$ 0	111 $\pm$ 31	ND	ND
July 1990	7	11 $\pm$ 6	29 $\pm$ 17	<1	74 $\pm$ 27
September 1990 #1	4	8 $\pm$ 3	149 $\pm$ 35	9 $\pm$ 5	28 $\pm$ 13
September 1990 #2	5	12 $\pm$ 3	232 $\pm$ 89	9 $\pm$ 4	57 $\pm$ 21

June, 1987, data previously published (Vetter *et al.*, 1989). Values are mean $\pm$ standard deviation.

"ND" represents value not determined.

a single grab, 20 clams were placed in oxic seawater containing no reduced sulfur substrates. The removal of thiols from the blood of the clams is shown in Table II. An initial thiosulfate concentration of $274 \pm 106 \mu M$ decreased to $17 \pm 11 \mu M$ in 12 h and to zero in 24 h. Low concentrations of sulfide and sulfite were also cleared from the blood within 12 h while glutathione concentrations remained relatively constant.

Aerobic and anaerobic metabolism of sulfide and thiosulfate by whole animals

Sulfide and thiosulfate uptake and metabolism under oxic conditions were investigated using aquarium-maintained clams. Incubations with whole clams were for either 2 or 4 h. The animals were incubated in 500 ml filtered seawater at $10^\circ C$ in the presence of either sulfide or thiosulfate.

Table II

Clearance of sulfur compounds from the blood of freshly collected *Solemya reidi* during an incubation in sulfide-free, oxygenated seawater

Sample	n	Sulfur compounds (μM)			
		Sulfide	Thiosulfate	Sulfite	Glutathione
T = 0 h	4	9 $\pm$ 1	274 $\pm$ 106	13 $\pm$ 1	19 $\pm$ 24
T = 6 h	4	17 $\pm$ 8	66 $\pm$ 44	27 $\pm$ 10	27 $\pm$ 29
T = 12 h	4	0 $\pm$ 0	17 $\pm$ 11	0 $\pm$ 0	9 $\pm$ 0
T = 24 h	4	0 $\pm$ 0	0 $\pm$ 0	2 $\pm$ 3	11 $\pm$ 2
T = 96 h	4	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	18 $\pm$ 5

Values are mean $\pm$ standard deviation.

Whole clams incubated with sulfide ($100 \mu M$) showed very little sulfide or sulfite accumulation in the blood during the 2-h experiment (Table III). However, high concentrations of thiosulfate in the blood were observed. To examine the possibility that thiosulfate was actively transported by the clam, a thiosulfate ratio representing the ratio of the seawater thiosulfate concentration at the end of each incubation to the thiosulfate concentration in the blood at the end of each incubation was calculated. The thiosulfate ratio under oxic conditions was 1:300. Glutathione concentrations did not show any consistent pattern.

Similar experiments were performed by incubating clams with thiosulfate. Under these conditions, the clams did not concentrate thiosulfate in their blood above the concentration in the surrounding seawater during 2- and 4-h incubations with two thiosulfate concentrations (50 and $250 \mu M$) (Table III). The thiosulfate ratio for either concentration was never greater than 1:1. Virtually no sulfide or sulfite was observed in the blood and glutathione again showed no consistent patterns.

We also investigated whole animal sulfide and thiosulfate metabolism under anoxic conditions. In these experiments, whole clams were incubated in seawater that was sparged with argon. Anoxic conditions were maintained throughout the incubations.

Anoxic incubations of clams with sulfide ($100 \mu M$) showed little sulfide or sulfite accumulation in the blood (Table III). However, unlike oxic incubations, blood thiosulfate concentrations did not increase substantially ($24 \mu M$ as compared to $300 \mu M$ during anoxic incubations).

Thiosulfate was removed from the seawater and appeared in the blood of animals incubated under anoxic

Table III

Sulfur compounds from blood of Solemya reidi after oxid and anoxic incubations with sulfide and thiosulfate. All incubations were in 500 ml seawater at 10°C

Incubation conditions	n	Sulfur compounds (μM)				Thiosulfate ratio*
		Sulfide	Thiosulfate	Sulfite	Glutathione	
Sulfide						
Oxic—2 h						
Control	4	0 $\pm$ 0	18 $\pm$ 1	0 $\pm$ 0	13 $\pm$ 10	
100 μM	6	1 $\pm$ 1	300 $\pm$ 217	1 $\pm$ 1	15 $\pm$ 5	1:300
Anoxic—2 h						
Control	4	8 $\pm$ 3	8 $\pm$ 5	4 $\pm$ 3	9 $\pm$ 7	
100 μM	6	6 $\pm$ 2	24 $\pm$ 23	7 $\pm$ 1	33 $\pm$ 19	1:24
Thiosulfate						
Oxic—2 h						
Control	3	2 $\pm$ 2	5 $\pm$ 3	4 $\pm$ 1	9 $\pm$ 10	
250 μM	3	4 $\pm$ 1	136 $\pm$ 0	7 $\pm$ 3	38 $\pm$ 9	1:0.8
Oxic—4 h						
250 μM	3	3 $\pm$ 2	152 $\pm$ 4	6 $\pm$ 4	38 $\pm$ 2	1:0.9
Oxic—2 h						
Control	4	2 $\pm$ 2	22 $\pm$ 13	12 $\pm$ 4	28 $\pm$ 20	
50 μM	4	3 $\pm$ 5	35 $\pm$ 11	9 $\pm$ 9	16 $\pm$ 4	1:0.8
250 μM	4	0 $\pm$ 0	157 $\pm$ 17	3 $\pm$ 2	11 $\pm$ 1	1:0.8
Anoxic—2 h						
Control	3	2 $\pm$ 2	5 $\pm$ 3	4 $\pm$ 1	9 $\pm$ 10	
250 μM with 5 mM nitrate	3	6 $\pm$ 2	158 $\pm$ 63	4 $\pm$ 1	14 $\pm$ 12	1:0.7
250 μM w/out 5 mM nitrate	3	3 $\pm$ 2	116 $\pm$ 33	4 $\pm$ 2	25 $\pm$ 19	1:0.5

Sulfur compound values are mean $\pm$ standard deviation.

* The thiosulfate ratio represents the ratio of the seawater concentration at the end of each incubation to the concentration in the blood. The concentration of thiosulfate in the seawater at the end of the sulfide incubations was below the limits of detection, thus a value of 1 μM was assigned. Controls represent animals after oxid or anoxic incubations without a reduced sulfur substrate (either sulfide or thiosulfate).

conditions both with and without nitrate (Table III). The pattern of blood thiols under anoxic conditions was similar to that for oxid conditions. Thiosulfate was not concentrated in the blood above the concentrations of the surrounding seawater under any of the incubation conditions.

Sulfide and thiosulfate stimulated nitrate/nitrite respiration

The intact symbiosis exhibited nitrate respiration under oxid and anoxic conditions in the presence of sulfide and thiosulfate (Fig. 1a, b). In the presence of 5 mM nitrate, nitrite accumulated in filtered seawater during 3-h oxid incubations with whole clams in the presence of 150 μM sulfide and 250 μM thiosulfate (Fig. 1a). Two different controls were run to confirm that nitrate respiration was being carried out by the symbiotic bacteria. First, 5 mM nitrate was added to filtered seawater containing 150 μM sulfide without clams. No nitrite accumulated in the seawater (not shown). Second, 5 mM nitrate was added to filtered seawater containing clams and no sulfide (Fig. 1a). Blood nitrite concentrations at the end of the 3-h incubations were 158 $\pm$ 80 μM (n = 4) and 52 $\pm$ 16 μM

(n = 4) for sulfide- and thiosulfate-incubated clams, respectively.

Anoxic incubations were also performed. Whole clams had the potential for nitrate respiration under anoxic conditions (Fig. 1b). Three different controls were run. First, 5 mM nitrate was added to filtered, deoxygenated seawater containing 150 μM sulfide without clams. No nitrite accumulated in the seawater (Fig. 1b). Second, no nitrate was added to filtered, deoxygenated seawater containing 250 μM thiosulfate with clams. No nitrite accumulated in the seawater (data not shown). Finally, 5 mM nitrate was added to filtered, deoxygenated seawater containing 150 μM sulfide with clams that had their gills removed. Very little nitrite (2.0 $\pm$ 0.2 μM) accumulated in the seawater (Fig. 1b). Blood nitrite concentrations at the end of 3-h incubations were 214 $\pm$ 103 μM (n = 4) and 189 $\pm$ 80 μM (n = 4) for sulfide- and thiosulfate-incubated clams, respectively.

Five mM nitrate concentrations are not environmentally realistic. Because nitrite accumulation (*versus* nitrate disappearance) was measured and nitrite only accumulated in the presence of excess nitrate, it was essential that excess nitrate be available to the clams during the entire

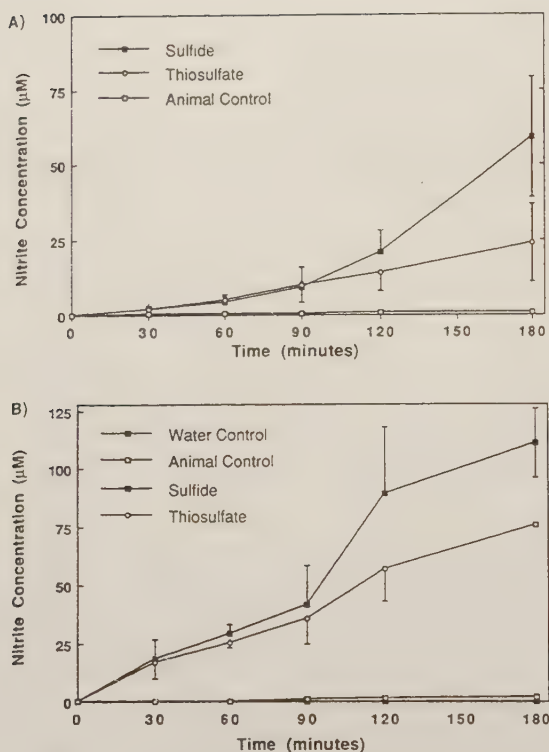


Figure 1. Nitrate respiration of whole *Solemya reidi* during 3-h incubations in oxic and anoxic buffered seawater at 10°C. (A) Nitrite accumulation in oxic seawater during incubations containing 5 mM nitrate and either 150 μ M sulfide (mean $\pm$ standard deviation of 4 incubations) or 250 μ M thiosulfate (mean $\pm$ standard deviation of 4 incubations). The animal control represents seawater containing 5 mM nitrate, animals, and no sulfide. (B) Nitrite accumulation in anoxic seawater during incubations containing 5 mM nitrate and either 150 μ M sulfide (mean $\pm$ standard deviation of 4 incubations) or 250 μ M thiosulfate (mean $\pm$ standard deviation of 4 incubations). The water control represents seawater containing 5 mM nitrate, 150 μ M sulfide, and no animals. The animal control represents seawater containing 5 mM nitrate, 150 μ M sulfide, and 4 animals with their gills removed. Clam size ranged from 32 to 42 mm and all values are normalized to a wet gill weight of 420 mg/clam.

3-h incubation. However, whole animal nitrate respiration (nitrite accumulation) rates similar to those presented above were found when clams were incubated in 500 μ M and 50 μ M nitrate for short incubations (only single experiment—data not shown). Similar results have also been found for bacterial preparations (Javor, pers. comm.).

The intact symbiosis showed nitrite respiration under anoxic conditions in the presence of sulfide but not thiosulfate (Fig. 2). In the presence of 150 μ M sulfide, 100 μ M nitrite was removed from filtered seawater by whole clams incubated anoxically. An initial nitrite concentra-

tion of $101.5 \pm 2.8 \mu$ M decreased to $69.9 \pm 6.0 \mu$ M during a 3-h incubation. Two different controls were run to confirm that nitrite respiration, like nitrate respiration, was being carried out by the symbiotic bacteria. First, 100 μ M nitrite was added to filtered, deoxygenated seawater containing 150 μ M sulfide and no clams. The seawater nitrite concentration did not decrease (Fig. 2). Second, nitrite was added to filtered, deoxygenated seawater containing no reduced sulfur compound and three clams. Again, the seawater nitrite concentration did not decrease (data not shown). Blood nitrite concentrations at the end of 3-h incubations were $5.3 \pm 2.5 \mu$ M and $17.3 \pm 4.6 \mu$ M for sulfide and thiosulfate incubations, respectively.

Sulfide-stimulated oxygen consumption by bacterial symbionts

The whole animal experiments could not directly address the question of whether the bacteria could carry out respiratory sulfide oxidation. To determine if the symbionts could respire sulfide aerobically, we measured azide-sensitive (respiratory) and azide-insensitive (non-respiratory) oxygen consumption of bacterial suspensions in the presence of different sulfide concentrations. The bacterial suspensions contained granules because they could not be separated from the bacteria. The suspensions oxidized a wide range of sulfide concentrations with maximal respiration rates at 25 μ M sulfide (Fig. 3a). A pairwise comparison of values at 25 μ M and all higher concentrations using the Mann-Whitney U test (Zar, 1984) found no significant difference between 25 μ M and any higher values ($P > 0.05$). However, the number of repli-

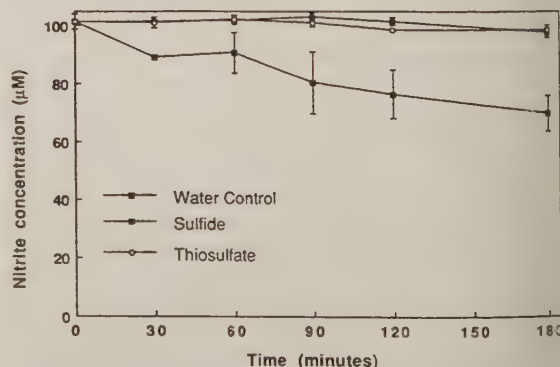


Figure 2. Nitrite respiration of whole *Solemya reidi* during 3-h incubations in anoxic buffered seawater at 10°C. Nitrite disappearance in seawater during incubations containing either 200 μ M sulfide (mean $\pm$ standard deviation of 4 incubations) or 200 μ M thiosulfate (mean $\pm$ standard deviation of 4 incubations). The water control represents seawater containing 100 μ M nitrite, 150 μ M sulfide, and no clams. Clam size ranged from 32 to 42 mm and all values are normalized to a wet gill weight of 420 mg/clam.

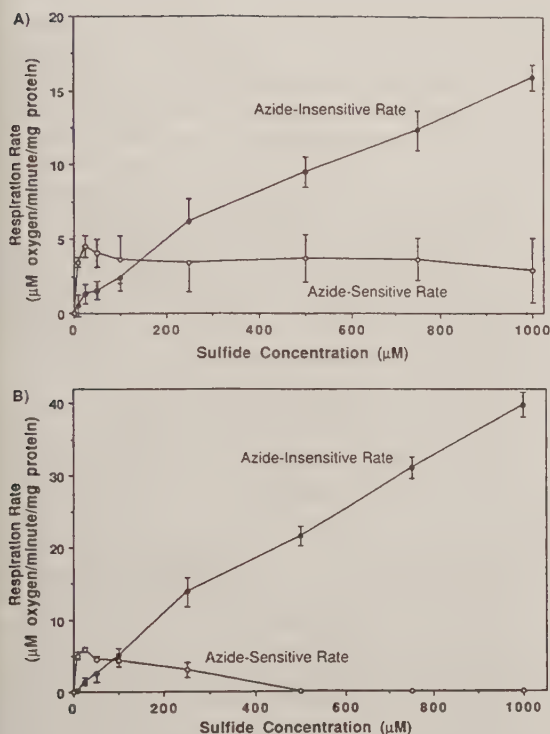


Figure 3. Sulfide-stimulated oxygen consumption in buffered sea water at 15°C by bacterial enrichments from (A) the gills of mud-maintained *Solemya reidi* or (B) the gills of clams maintained in oxygenated seawater that contained no reduced sulfur compounds or nitrate for 21 days. Data points represent means and standard deviations from three experiments ($n = 3$). See Materials and Methods for clam size and bacterial density.

cates ($n = 3$) is not sufficient for a robust statistical determination. Thus, aerobic respiration was apparently not inhibited by sulfide concentrations up to 1 mM. However, the azide-insensitive oxygen consumption rate increased over the range of sulfide concentrations tested. The maximal rate for azide-insensitive consumption was above 1 mM. The data in Figure 3a are the combination of the means from multiple measurements in three different experiments (each experiment was done with one bacterial preparation consisting of many clams).

Similar respiration experiments were conducted on bacterial suspensions from clams that were maintained in oxygenated seawater without an external reduced sulfur source or nitrate for three weeks. The gills of these animals were dark (no yellow sulfur globules). The total number of bacteria or a bacteria to granule ratio was not determined. However, it has been observed that starved clams have more granules than healthy clams (pers. obs.). The

bacterial suspensions from these gills showed a different pattern for azide-sensitive and insensitive oxidation rates (Fig. 3b). Azide-sensitive aerobic respiration again had a maximum rate at 25 μM , but appeared to be inhibited at higher concentrations with complete inhibition at 500 μM and greater sulfide concentrations. The azide-insensitive rate increased with increasing sulfide concentrations and was more than double that found in the bacterial enrichments from animals freshly removed from mud based on total protein of the suspensions. The data in Figure 3b are the combination of three different experiments.

Discussion

Analysis of sediment porewaters showed that sulfide was typically the only reduced sulfur compound available to *S. reidi* and that concentrations ranged from below 20 μM to nearly 1 mM. Because the clams actively pump water from above the sediment through their burrows, sulfide concentrations in the water that is in contact with the gills may be significantly lower. Porewater thiosulfate was present in extremely low concentrations, and the clams were unable to accumulate thiosulfate in the blood above the external concentration. Thus, it appears that porewater thiosulfate is of little importance as an energy source in the intact symbiosis.

Similar to Anderson *et al.* (1987), we observed high concentrations of thiosulfate in the blood of field caught animals and animals experimentally incubated in the presence of sulfide. Our data show that thiosulfate present in the blood of freshly collected clams results from host oxidation of sulfide and not from uptake of porewater thiosulfate. Because thiosulfate accumulates in the blood during oxic incubations with sulfide but not during anoxic incubations, molecular oxygen must be required for sulfide oxidation to thiosulfate. It is most likely that aerobic respiration of sulfide by mitochondria is responsible for thiosulfate production (O'Brien and Vetter, 1990). Thiosulfate is cleared from the blood by the bacteria within bacteriocytes. However, the relative importance of this energy source *versus* direct uptake of sulfide across the gill is not known.

Two clearly different types of sulfide oxidation occurred in our bacterial enrichments. The first, true respiration, represents electron transport chain (ETS)-linked bacterial sulfide oxidation and it is completely azide-sensitive. The ETS-linked type showed a high capacity to oxidize sulfide at low concentrations (maximal rate by 25 μM). The second, which is azide-insensitive, represents non-enzymatic oxidation by ferric iron catalysis (hematin) in granules (Powell and Arp, 1989) and autocatalysis by sulfur (Chen and Morris, 1972).

Non-enzymatic, heat-stable catalysis of sulfide oxidation has been observed in a variety of animal tissues (re-

viewed by Beauchamp *et al.*, 1984) and specifically in a thiotrophic symbiosis (Wilmot and Vetter, 1990). It has been shown that ferric iron-containing compounds such as hematin and ferritin are responsible for the non-enzymatic catalysis in mammals (Sörbo, 1958; Baxter and van Reen, 1958; Baxter *et al.*, 1958). The benzyl viologen (BV) assay used to determine which components of the *S. reidi* symbiosis carried out sulfide oxidation (Powell and Somero, 1985) measures non-enzymatic ferric iron catalysis in the presence of high (1–5 mM) sulfide (Powell and Arp, 1989). It does not measure ETS-linked activity because high sulfide concentrations inhibit the oxidation. Thus, it is not surprising that early studies using the BV assay concluded that the bacteria and mitochondria did not oxidize sulfide (Powell and Somero, 1985).

Although we have shown that the bacteria are capable of sulfide oxidation, it is not clear whether the bacteria encounter sulfide or if it is first oxidized by mitochondria or electron-dense granules. Several lines of evidence suggest that the bacteria normally oxidize sulfide as well as thiosulfate *in vivo*. First, the bacteria are oriented close to the outside and are separated from the seawater by a thin epithelial cell that contains few mitochondria or electron-dense granules (Felbeck, 1983; Gustafson and Reid, 1988). Because the bacteria are not packed close to the blood space, which contains the mitochondrial product of sulfide oxidation, it does not seem likely that thiosulfate is the only sulfur substrate available to the bacteria. Second, isolated gill ctenidia can oxidize sulfide without a host blood supply (Vetter, 1990). The ctenidia produce elemental sulfur and protein, which seems to indicate that sulfide and oxygen are taken directly across the gill (Vetter, 1990). Third, the bacteriocytes of *S. reidi* and *S. velum* contain intracellular hemoglobin that can bind sulfide as ferric hemoglobin sulfide (Doeller *et al.*, 1988; Krause and Wittenberg, 1990). Fiber-optic spectroscopy of intact gills indicated that ferric hemoglobin sulfide was present in the bacteriocyte region of the gill.

The data presented above do not provide direct proof that the bacteria within a bacteriocyte oxidize sulfide. Javor (pers. comm.) has recently observed that bacterial suspensions from *S. reidi* respire nitrate under oxic and anoxic conditions in the presence of sulfide and thiosulfate. Similarly, in this study, the symbionts respired nitrate that entered the bacteriocyte, either from the blood, or directly from seawater in the presence of sulfide and thiosulfate. The product of the anaerobic respiration, nitrite, was excreted from the bacteriocyte in the presence of excess nitrate and accumulated in the blood and seawater. In marine denitrifying bacteria, nitrate is often reduced only to nitrite (Goering and Cline, 1970) and the nitrite accumulates outside the cells (Payne and Riley, 1969). If nitrate concentrations become low or are exhausted, the

nitrite can be taken back up by the bacteria and further reduced.

In the absence of nitrate, the intact symbiosis respired nitrite in the presence of sulfide only. This has also been observed for bacterial suspensions from *S. reidi* (Javor, pers. comm.). The nitrite, like the nitrate, either enters the bacteriocyte from the blood or directly from seawater. More importantly, these data provide the best available evidence that the bacteria within bacteriocytes oxidize sulfide. These results suggest that sulfide oxidation is coupled to complete denitrification, but that thiosulfate oxidation is coupled to the first step only. Anaerobic sulfide oxidation by the bacteria may be an important detoxification mechanism when the clam is depleted of oxygen. In addition, because aerobic nitrate respiration has been described for several bacteria (Robertson and Kuenen, 1984; Lloyd *et al.*, 1987) denitrification may occur when nitrate (and sulfide) is present and oxygen concentrations are low.

Although the symbionts are capable of denitrification, and the bacteria have access to nitrate and nitrite when each is present in seawater, we do not know the concentrations that are available to the animals in the natural environment. The water flow across the sludge field is strong and the oxygen concentrations and water chemistry are similar to the surrounding areas (approximately 100–175 $\mu\text{M O}_2$) (B. Thompson, pers. comm.). At neighboring hydrographic stations in the Santa Monica Bay area, the ammonia concentrations range from 0.5 to 2.0 μM , while sediment porewaters typically are 100–1000-fold higher (Eppley, 1986). Nitrifying bacteria are active in these waters (Ward *et al.*, 1982) and nitrate values at a depth equal to the sludge field are $\geq 20 \mu\text{M}$ (Williams, 1986). Nitrate is not present below the top 2 cm of sediment at Whites Point outfall near the Hyperion outfall (J. Gieskes, pers. comm.). It can be assumed that as the clams pump water from above the sediment through their burrows, they are probably exposed to oxygen and nitrate simultaneously, but the ratio of oxygen to nitrate is unknown.

When the data presented here are integrated with previous studies (Felbeck, 1983; Powell and Somero, 1985, 1986; Fisher and Childress, 1986; Anderson *et al.*, 1987, 1990; Doeller *et al.*, 1988; Krause and Wittenberg, 1990; O'Brien and Vetter, 1990), a more complete picture emerges of how the symbiosis may be functioning under different environmental conditions. Maximum net autotrophy occurs in the presence of external sulfide concentrations of 100 μM (Anderson *et al.*, 1987). Because seawater is near pH 8.1 at 100 μM total sulfide, approximately 3 μM sulfide as H_2S diffuses into animal cells (Millero, 1986). Assuming an internal pH near pH 7.5 the maximal internal free sulfide (H_2S) concentration is approximately 20 μM , which is very close to the aerobic sulfide-oxidizing maximum for both isolated mitochondria

dria (O'Brien and Vetter, 1990) and bacteria. Aerobic metabolism is maintained by animal tissues in the presence of external sulfide concentrations up to 100 μM . At higher concentrations, the onset of anaerobic pathways is evident (Anderson *et al.*, 1990).

Sulfide oxidation can occur by at least two processes: sulfide respiration by mitochondria and bacteria, and non-enzymatic catalysis by metal containing granules, and autocatalysis by sulfur. The mitochondria oxidize sulfide only to thiosulfate which accumulates in the clam's blood (O'Brien and Vetter, 1990). The oxidation is oxygen-dependent and can yield ATP (Powell and Somero, 1986). Presumably, the bacteria oxidize sulfide to elemental sulfur and polysulfides and ultimately to sulfate. Bacterial sulfide respiration can occur aerobically when oxygen is available or possibly anaerobically when nitrate (or nitrite) is available as an alternate electron acceptor. The importance of nitrate (nitrite) respiration is unknown. In addition, the thiosulfate produced by the mitochondria can be further oxidized by the bacteria. The importance of the non-enzymatic oxidation of sulfide is unknown.

We have shown the metabolic potential for the use of nitrate and nitrite as alternate electron acceptors in the intact symbiosis. Future studies must determine the environmental concentrations of nitrate, nitrite, and oxygen and the relevance of anaerobic respiration to the symbiosis. If oxidized nitrogen compounds are present, they are likely in the oxygen-containing water drawn into the burrow by the clams. Thus, conditions that limit oxygen availability would also limit nitrate. A reasonable hypothesis may be that a switch to anaerobic nitrogen respiration by the symbionts is a tactic by the symbiosis to save oxygen for host metabolism during times of low oxygen.

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PACIFIC SARDINE

History of the Fishery

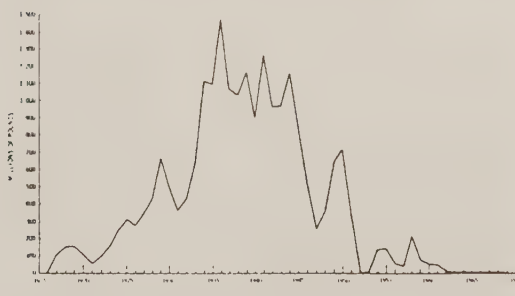
A sustained fishery for Pacific sardines (*Sardinops sagax*) first developed in response to the demand for food during World War I. Demand grew, and fishing effort and landings increased from 1916 to 1936, when the catch peaked at over 700,000 tons. The Pacific sardine supported the largest fishery in the western hemisphere during the 1930's and 1940's, with landings occurring in British Columbia, Washington, Oregon, and California. The fishery collapsed beginning in the late 1940's and declined, with short term reversals, to less than 1,000 tons per year in the late 1960's. There was a southward shift in the catch as the fishery decreased, with landings ceasing in the northwest in the 1947-1948 season and in San Francisco in 1951-1952. Through the 1945-1946 season, most California landings were at Monterey and San Francisco, but San Pedro accounted for most subsequent landings.

Sardines were used primarily for reduction to fish meal and oil and canned for human consumption, with small quantities taken for live bait. Although most fish landed north of California were reduced, California processors began as canners, and expanded to reduction as a lucrative supplement. Reduction was often more profitable, and for many years reduction tonnage exceeded tonnage canned. An extremely lucrative dead bait market for sardines developed in central California in the 1960's and was primarily responsible for continued fishing on the depleted resource.

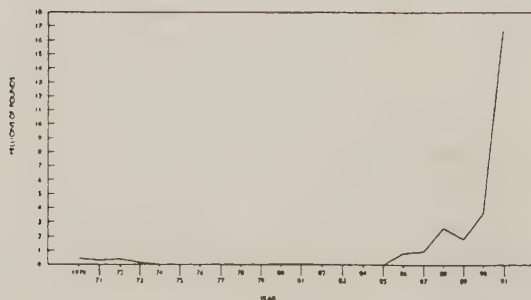
Prior to 1967, management of the sardine resource in California was mostly limited to: 1) control of tonnage of whole fish used for reduction, 2) case pack requirements (specified number of cases of canned fish per ton of whole fish), and 3) restriction of the fishing season. The first two controls were intended to lower the quantity of sardines used for reduction,

since this was regarded as a less desirable use and demand for reduction products was high. The latter control was designed to limit canning to periods when sardines were in prime condition and to improve the market for canned products. The total catch, however, was not regulated. From 1967 to 1973, California landings of sardines were limited to an incidental take of 15 percent sardines by weight mixed with other fish. Liberal provisions for use of incidental catch, and later a 250-ton dead bait quota, still supplied the demand for bait. In 1974, a moratorium on fishing sardines was established, which restricted landings to the 15 percent incidental limit and eliminated the use of sardines for dead bait. This legislation also established the state's intent to rehabilitate the resource. Through 1981, sardine landings were less than 50 tons per year.

Since the early 1980's, sardines have been taken incidentally in the southern California fishery for Pacific and jack mackerel. Most sardines from this source were canned for pet food, with a lesser amount canned for human consumption. A small directed fishery for sardines has been permitted annually since 1986. The quota (excluding bait fisheries) was limited to 1,000 tons per year from 1986 through 1990, and was increased to 8,150 tons in 1991. Sardines landed in the directed fisheries in southern and central California are primarily canned for human consumption and sold overseas, with minor amounts sold fresh for human consumption and animal food. Small quantities are harvested for dead bait and live bait. No reduction of sardines, except of waste produced from other processing operations, is currently taking place in California. Total annual landings of sardines have increased, from less than 100 tons in the 1970's and early 1980's, to 1,283 tons in 1986, and 8,543 tons in 1991.

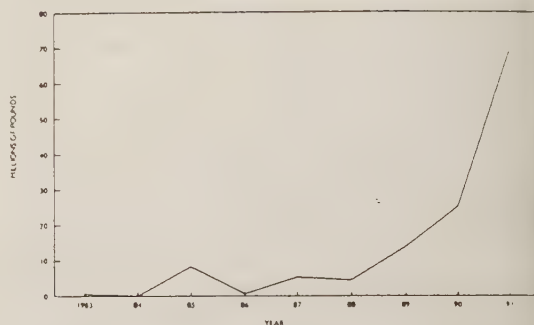


California commercial landings of Pacific sardine, 1916-1969.



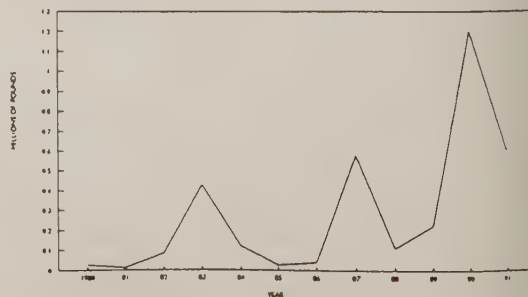
Commercial landings of Pacific sardine, 1970-1991.

Landings of sardines in Mexico have increased steadily during the 1980's, and were similar in magnitude to California landings through 1990. In 1991, however, sardine landings in Ensenada totaled 34,600 tons. Sardines landed in Mexico prior to 1991 were used for canning and reduction. In 1991, most sardines were used for reduction. The recent increase in sardine landings has been due in part to a decline in the availability of anchovies.



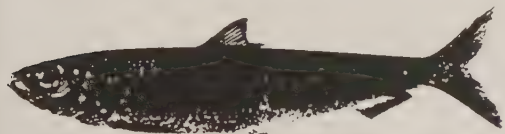
Commercial landings of Pacific sardine in Ensenada, Mexico, 1983-1991.

A fishery management plan for coastal pelagic species, including sardines, is being developed by the Pacific Fishery Management Council. Until the new management plan is adopted, the sardine fishery in California will continue to be managed by the state. Current state regulations provide for a 1,000-ton directed fishery when the spawning biomass is greater than 20,000 tons. This quota may be increased as warranted, provided any increase is consistent with the continued growth and rehabilitation of the resource. A quota of 250 tons (500 tons when the directed quota is 2,500 tons or greater) is reserved for dead bait. The live bait quota may be increased above a minimum level of 350 tons if such increase is consistent with the continued rehabilitation of the resource. At present, the live bait quota is 1,000 tons. Incidental take (in effect when directed or dead bait quotas are filled) is presently limited to 35 percent by weight. Current policy limits the total annual harvest of sardines to 10 percent of the spawning biomass. The sardine resource will be considered to be rehabilitated when the spawning biomass is at least one million tons, the population occupies much of its former range, and the age structure of the population resembles that of the population during previous periods of high abundance.



California landings of Pacific sardine for live bait, 1980-1991.

The price of sardines landed incidentally with mackerel decreased from about \$190 per ton in the mid 1980's to about \$150 per ton in 1991. The price for sardines landed in the directed fishery and canned for human consumption has ranged from \$80 to \$105 per ton. Only limited markets exist for canned products currently being produced. The traditional wetfish fleet and processing sector are in poor economic condition and have not successfully developed new products or markets. It remains to be seen whether markets will develop to utilize a fully-recovered population of Pacific sardines.



Pacific sardine, *Sardinops sagax*.

Status of Biological Knowledge

Sardines are small pelagic fish and members of the herring family. The genus *Sardinops* occupies the coastal areas of warm temperate zones of nearly all ocean basins. The genus is considered monotypic, and *Sardinops sagax* is the correct scientific name for sardine populations in the Alguhas, Benquela, California, Kuroshio, and Peru currents, and for populations off New Zealand and Australia. In the northeast Pacific Ocean, as in most other areas, the Pacific sardine occurs with anchovy, hake, and mackerel. It is generally accepted that the Pacific sardine population consists of three subpopulations or stocks: a Gulf of California subpopulation, a southern subpopulation off Baja California, and the principal northern subpopulation ranging from northern Baja California to Alaska. These stocks were distinguished on the basis of serological techniques. A fourth, far northern subpopulation was also postulated. Recent electrophoretic studies and examination of morphological variation showed no genetic variation among sardines from central and southern California, the Pacific coast of Baja California and the Gulf of California.

Historically, the northern subpopulation of sardines made extensive migrations, moving north as far as British Columbia in the summer months and returning south to southern California and northern Baja California in the fall. Northward movement was greater with increased age. The migration was complex, and the timing and extent of movement were affected to some degree by oceanographic conditions. At present, the population is relatively small, and is found primarily off central and southern California and Baja California. Contraction of range and spawning area has been associated with decreases in sardine population size around the world.

Estimates of sardine abundance from A.D. 280 to 1970 have been derived from the deposition of fish scales in sediment cores from the Santa Barbara Basin. Significant sardine populations existed throughout the time period and varied widely in size, typically over periods of roughly 60 years. Population

declines and recoveries averaged about 36 and 30 years, respectively. Scale data indicate that sardine populations were much more variable than anchovy populations. Studies of deposits of otoliths have shown that, while the anchovy has been present for a million years or more, no trace of sardines has been found that is more than seven thousand years old. The tendency for tremendous variations in sardine biomass may be a characteristic of a species that has only recently occupied its habitat.

Pacific sardines reach about 16 inches and live as long as 13 years, but are usually less than 12 inches and eight years old. Most sardines in the historical and recent commercial catch were five years and younger. There is a good deal of regional variation in growth rate, with average size attained at a given age increasing from south to north. Sardine size and age at maturity may decline with a decrease in sardine biomass, although latitudinal and temperature effects may also play a part. At low biomass levels, sardines appear to be fully mature at age two, while at high biomass levels, only some of the two year olds are mature.

Sardines age three and older were nearly fully vulnerable to the historical fishery until 1953, but two and three year old fish became less available as the population declined and fewer southern fish moved northward. Recent catch data indicate sardines begin to become available to the fishery at age one, and are fully vulnerable by age three. Sardines probably become vulnerable to the live bait fishery, which is located close to shore, at a younger age.

Spawning occurs in loosely aggregated schools in the upper 165 feet of the water column, probably year-round, with peaks from April to August from Point Conception to Magdalena Bay, and from January to April in the Gulf of California. The main spawning area for the northern subpopulation is between Point Conception and San Diego, out to about 100 miles offshore, with evidence of spawning as far as 350 miles offshore. Historically, spawning also occurred off central California and may have been a fairly regular occurrence. Sporadic occurrences of spawning have been observed off Oregon and British Columbia.

Most spawning occurs between 55° and 63°F, with an apparent optimum between 59° and 61°F, and a minimum threshold temperature of 55°F. The spatial and temporal distribution of spawning is influenced by temperature; the center of sardine spawning has shifted northward and continued over a longer period of time during warm water conditions. Pacific sardines are serial spawners and spawn several times over a spawning season, although the number of spawnings is not known. Eggs and larvae are found near the surface. The eggs are spheroid, have a distinct, large perivitelline space, and require about three days to hatch at 59° F.

Recruitment of Pacific sardines is highly variable. Analyses of the stock-recruitment relationship have been inconclusive and controversial, with some studies showing a density-dependent relationship and others finding no relationship whatsoever. From 1932 to 1965, mean recruitment only slightly exceeded potential replacement of spawners at all levels of abundance, indicating little resilience to fishing. Recruitment occurs in strings, with several years of successful recruitment

followed by similar periods of poor recruitment. The timing and duration of these strings has a large effect on population growth.

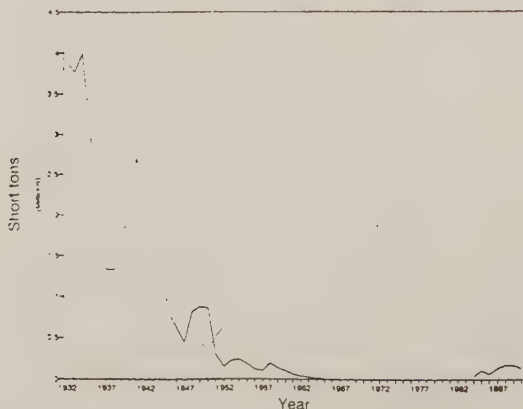
Sardines are filter feeders and prey on crustaceans, mostly copepods, and other plankton, including fish larvae and phytoplankton. Larval sardines feed extensively on the eggs, larvae, and juvenile stages of copepods, as well as other zooplankton and phytoplankton.

Through all life stages, sardines are eaten by a variety of predators. Eggs and larvae are consumed by an assortment of invertebrate and vertebrate planktivores. Although it has not been demonstrated in the field, anchovy predation on sardine eggs and larvae has been postulated as a possible mechanism for increased larval sardine mortality during the 1950's and 1960's. Juvenile and adult sardines are consumed by other fish, including yellowtail, barracuda, bonito, tunas, marlin, mackerel, hake, and sharks; sea birds, such as pelicans, gulls, and cormorants; and marine mammals, including sea lions, seals, porpoises, and whales. It is likely that sardines will become more important as prey for numerous species, including endangered species such as the California brown pelican, as the sardine resource continues to increase.

The Pacific sardine and other closely-related species undergo similar interannual changes in abundance in several other temperate coastal regions of the world. Scientists in several countries have conducted joint studies of recruitment and biomass of these coastal pelagic stocks under the Sardine-Anchovy Recruitment Program. Knowledge of the population dynamics and variability of these clupeoid fishes may eventually contribute to the detection of the oceanographic effects of global climate change.

Status of the Population

Spawning biomass of the Pacific sardine averaged 3,881,000 tons from 1932 to 1934, and fluctuated from 3,136,000 to 1,324,000 tons from 1935 to 1944. The population then declined steeply over the next two decades, with some short reversals following periods of particularly successful recruitment, to less than 100,000 tons in the early 1960's. During the 1970's, biomass levels were thought to be as low as 5,000 tons. Since the early 1980's, the sardine population has increased, and the spawning biomass in 1990 was estimated to be 130,000 tons.



Pacific sardine estimated biomass, 1932-1990.

Maximum sustained yield of Pacific sardine in the historical northern subpopulation was estimated to be 250,000 tons or about 22 percent per year, far less than the catch of sardines during the height of the fishery. Although combined landings in the U.S. and Mexico are still well below this level, landings have increased substantially in recent years. In the absence of a bilateral management agreement between the U.S. and Mexico, combined U.S. and Mexican catches of Pacific sardine may be high enough to retard the continued recovery.

Disagreement over whether the decrease in the sardine population was due to overfishing or to natural changes in the environment has persisted for many years. It is now apparent that both factors are important. Following the cessation of fishing and with the development of favorable environmental conditions, the sardine resource is recovering.

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Seasonal and Spatial Patterns of Ichthyoplankton Abundance in Elkhorn Slough, California

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Seasonal and spatial patterns in abundance of fish eggs and larvae are described from 323 samples collected from September 1974–September 1976 in Elkhorn Slough, a shallow, tidal embayment in Monterey Bay, California. These included 3645 larvae of 29 taxa that were numerically co-dominated by gobiid and clupeoid larvae. Ninety-four percent of the total catch comprised seven species, and included, in rank order abundance, *Gillichthys mirabilis*, *Engraulis mordax*, *Clevelandia ios*, *Hypomesus pretiosus*-osmerid, *Leptocottus armatus*, *Genyonemus lineatus*, and *Clupea pallasii*. Eggs of *E. mordax*, *Citharichthys* spp., and *G. lineatus* accounted for 73% of the catch.

Two seasonal groups of larvae were evident. *E. mordax* and the gobiids (*G. mirabilis* and *C. ios*) formed a summer–fall group. While more speciose, a winter and early-spring group comprised of larval *L. armatus*, *H. pretiosus*-osmerid, Atherinidae and *Ammodytes hexapterus* was not as abundant as the summer–fall assemblage. Egg densities were overwhelmingly high in summer, due almost entirely to *E. mordax*.

Similarity in species composition was greatest between collections from the most inland stations; larval assemblages from near-ocean stations were least similar to the inland slough assemblages. These distributions are attributed to reproductive specializations (egg type and spawning origin of adults) and hydrographic conditions.

Introduction

Early life of many nearshore marine fishes is spent in estuaries and shallow embayments (Pearcy & Myers, 1974; Weinstein, 1979; Powles *et al.*, 1984; Gunderson *et al.*, 1990). Year-class success of marine fish populations depends on survival during early developmental stages. Houde (1987) suggested relatively small variations in growth and mortality during early life may produce large fluctuations in fish recruitment. High prey availability,

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water temperature, and turbidity, and decreased water depth and turbulence in coastal embayments can enhance growth, limit predation, and increase the survival of young fishes (Blaber & Blaber, 1980; Blaber, 1985; McGowan, 1986). Many species are transient members of estuarine ichthyofauna, and transport primary production from these land-based ecosystems to coastal marine habitats after their first year of life (Weinstein & Walters, 1981; Allen, 1982). The contribution of these highly productive areas to coastal marine fish populations remains largely unknown.

Bays and estuaries of California are few in number and relatively small; their total area is less than 15% that of Chesapeake Bay (Horn & Allen, 1976). Greater than 75% of California's coastal wetlands have been lost through diking, filling, pollution and other degradations (Onuf *et al.*, 1978). Elkhorn Slough, a member of the National Estuarine Research Reserve System, is the largest wetland habitat south of San Francisco Bay on the central California coast. From studies of juvenile and adult fishes (Barry & Cailliet, 1981; Yoklavich *et al.*, 1991), the slough has been identified as spawning and nursery grounds for several species of marine fishes, as well as permanent home to at least six resident species. Although many of its resources are protected, continued erosion from breakage of dikes, wetland restoration activities, and strong tidal scour (Wong, 1989), and potential hydrographic and climatic changes (e.g. Onuf & Quammen, 1983) could impact this nursery area.

The principal objective of this study was to assess patterns of seasonal and spatial abundance of fish eggs and larvae in Elkhorn Slough. Additionally, we evaluate the influence of reproductive modes of adult fishes and physical characteristics of the environment on patterns of larval species composition. This study provides information prerequisite to long-term monitoring of ichthyoplankton assemblages in central California embayments, and for generating testable hypotheses regarding potential changes in these assemblages.

Study area

Elkhorn Slough (36°48'N, 121°47'W) is a shallow, tidal embayment and seasonal estuary at the head of the Monterey submarine canyon. It has an axial length of about 10 km, and a relatively small drainage basin of 585 km² (Figure 1; Browning, 1972). During our study, water depth of the main channel below mean lower low water (MLLW) ranged from about 5 m at the slough entrance to less than 2 m at the most inland station (Smith, 1973; Broenkow, 1977). Semidiurnal tides with a mean tidal range of 1.1 m result in well-mixed water in two environmentally distinct zones of the slough (Broenkow, 1977). The area above the mean tidal prism, which is about 4.8 km inland, has a water residence time in excess of 300 days. Salinity in this area varies seasonally with evaporation, precipitation and runoff, and ranges from 17‰ in March to 37‰ in June. Water temperature ranges from 12 to 26 °C. Water west of the tidal prism, representing about 75% of the mean high water volume, is exchanged daily and reflects nearshore ocean conditions, with cooler temperatures (12–18 °C) and more constant salinity (29–34).

Materials and Methods

Ichthyoplankton were collected monthly from September 1974–September 1976 at five stations located at the entrance to Moss Landing harbour, and approximately 0.6 (the bridge station), 3.1 (the dairy station), 5.4 (the red house station and present site of the

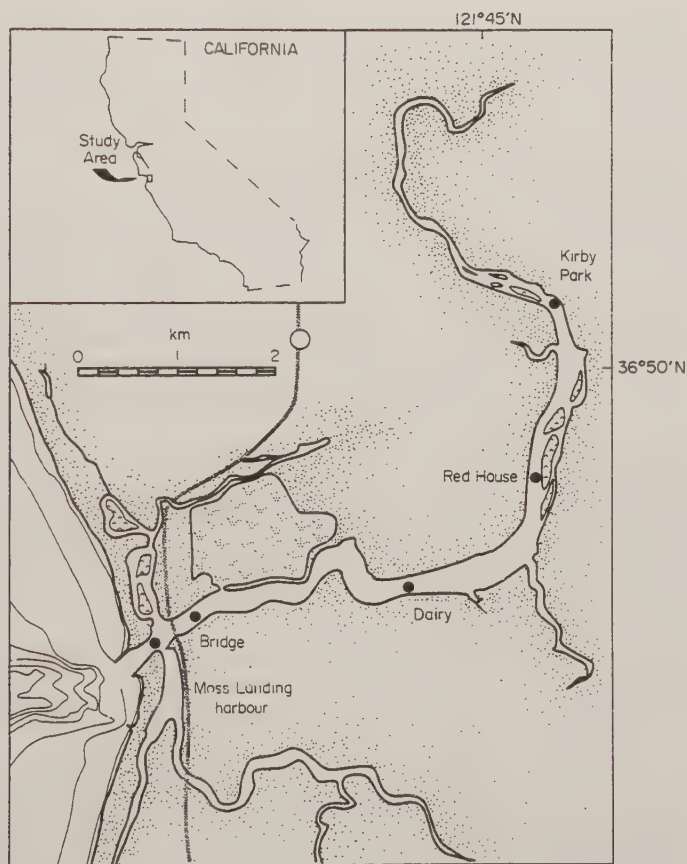


Figure 1. Larval fish sampling locations in Elkhorn Slough, CA.

Elkhorn Slough National Estuarine Research Reserve), and 7.9 km (the Kirby Park station) inland (Figure 1).

Larval fishes were collected with a 0.5 m diameter, 2.2 m long, zooplankton net (405 μ m mesh). The net was attached to a frame and pushed in front of a 5 m Boston Whaler, thereby reducing net avoidance and disturbance in shallow water. Mean filtering efficiency of the net was estimated with flow meters to be 89.1%, and was comparable to a suggested minimum value of 85% (Tranter & Smith, 1968). The net was fished mid-channel in a straight line between permanent station marks (137–297 m apart) at a constant speed (2 knots) and depth (about 1 m below the water's surface). Duration of each tow was recorded. Sampling was conducted during daytime in a specific sequence from the bridge to the Kirby Park station, and only at high slack tide to reduce the effect of tidal surge. The harbour entrance station was sampled on adjacent dates because we could not sample all five stations during a single high tide.

Initially, two replicate samples were collected at each station. After May 1975, four samples were taken each month because plots of cumulative number of species against a

randomly pooled number of samples indicated more replicates were needed to adequately sample all species. Dominant species, however, were not affected. Data were pooled by seasons, defined as fall (August, September, October), winter (November, December, January), spring (February, March, April), and summer (May, June, July). These groupings approximated the climatic seasonality of the study area in terms of rainfall, air and water temperature, and salinity (Broenkow, 1977).

Samples were preserved in the field with 10% formalin in seawater. Larval fishes were removed from all samples and stored in 5% buffered formalin. Fish eggs were sorted only from samples collected during the second year (October 1975–September 1976). Fish eggs and larvae were identified to the lowest taxa. Numbers of larvae of each species were standardized to 1000 m³ of water filtered. Density of eggs was expressed as number per m³. Larvae of good condition were measured to the nearest 0.5 mm (standard length).

We categorized larval species by egg types (demersal, pelagic and live-bearing) and spawning origin of the adult: resident (R: spawns and completes entire life in the slough); partial resident (PR: primarily lives in the slough, seasonally or ontogenetically moves to the ocean, and returns to reproduce in the slough); marine immigrant (MI: primarily lives in the ocean, and regularly spends some life stage in the slough); or marine (M: coastal species that rarely or never penetrates the inland slough area). Members of the R and PR categories potentially can spawn and complete their life cycle outside the slough environment. Studies on life histories of fishes in west coast estuaries (NOAA, 1990), and guides to early life stages of northeast Pacific fishes (Wang, 1981; Matarese *et al.*, 1989) were used to classify some species.

Species composition was compared between stations using the percentage similarity index (PSI; Krebs, 1989):

$$PSI = \sum \text{minimum}(p_{1i}, p_{2i})$$

where PSI is the sum of the smallest percentage by number (p_{1i} and p_{2i}) of each pair of species i from stations 1 and 2 respectively. This index ranges from 0.00 (no similarity) to 1.00 (identical species arrays). In the present study, PSI values greater than 0.60 were interpreted as significant, based on level of significance of product-moment correlation coefficient relative to PSIs (Cailliet & Barry, 1978). Additionally, Spearman's rank correlation coefficient, r_s (Sokal & Rohlf, 1981) was used to statistically compare rank order of species abundance between pairs of stations.

Results

Distribution and abundance of larvae

A total of 3645 larval fishes, representing 29 taxa from at least 17 families, was collected in 323 tows at five stations in Elkhorn Slough and adjacent harbour area. The only identifiable osmerids were post-flexion larval and juvenile *Hypomesus pretiosus* (surf smelt). We assumed younger larval osmerids were of this species also, but classified all as *H. pretiosus*-osmerid complex. Atherinid fishes probably included larvae of both species that spawn in the slough, *Atherinops affinis* (topsmelt) and *Atherinopsis californiensis* (jack smelt).

Seven species accounted for 94.0% of all larvae taken throughout the study (Table 1). The family Gobiidae comprised over 50% of the total catch; *G. mirabilis* (longjaw mudsucker) were the most abundant larvae.

Species composition and abundance varied seasonally and spatially. The greatest number of species occurred at the harbour entrance station, where 501 larvae of 20 taxa were

TABLE 1. Rank order abundance and size of fish larvae collected in Elkhorn Slough from September 1974 to September 1976. Adult life style was categorized as resident (R), partial resident (PR), marine immigrant (MI), and marine (M). Egg type of the adult was classified demersal (D), pelagic (P), or live-bearing (LB)

Taxa	Total catch		Modal		Length range (mm)	Adult life style	Egg type
	N	%	Length (mm)	Frequency (%)			
<i>Gillichthys mirabilis</i>	1476	40.5	3	95.7	2-8	R	D
<i>Engraulis mordax</i>	864	23.7	3	15.7	2-33	MI	P
<i>Clevelandia ios</i>	353	9.7	3	59.7	2-15	R	D
<i>Hypomesus pretiosus-osmerid</i>	220	6.0	4	35.9	3-50	MI	D
<i>Leptocottus armatus</i>	206	5.7	5	31.0	3-11	R	D
<i>Genyonemus lineatus</i>	162	4.4	2	73.5	2-4	M	P
<i>Clupea pallasii</i>	144	4.0	6	14.7	3-28	MI	D
<i>Neoclinus uninotatus</i>	42	1.2	4	97.2	4-5	M	D
<i>Citharichthys</i> spp.	33	0.9	2	100.0	2	MI	P
Atherinidae	31	0.9	8	48.2	5-10	PR	D
<i>Ammodytes hexapterus</i>	20	0.5	4	85.7	4-5	M	D
Clinidae type I	11	0.3	3	57.1	3-4	?	D
Gobiidae type I	8	0.2	3	50.0	2-4	R	D
<i>Sebastes</i> spp.	8	0.2	3	62.5	3-21	M	LB
<i>Stenobranchius leucopsarus</i>	3	0.1	4	60.0	4-5	M	P
<i>Psettichthys melanostictus</i>	2	0.1	3	100.0	3	M	P
<i>Coryphopterus nicholsi</i>	1	—	2	100.0	2	M	D
Gobiidae type II	1	—	4	100.0	4	R	D
<i>Clinocottus</i> sp.	1	—	4	100.0	4	M	D
<i>Gibbonsia</i> sp.	1	—	10	100.0	10	M	D
<i>Cebidichthys violaceus</i>	1	—	9	100.0	9	M	D
<i>Sebastes paucispinis</i>	1	—	3	100.0	3	M	LB
<i>Platichthys stellatus</i>	1	—	6	100.0	6	MI	P
<i>Lyopsetta exilis</i>	1	—	3	100.0	3	M	P
<i>Pleuromichthys verticalis</i>	1	—	3	100.0	3	M	P
<i>Bathylagus ochotensis</i>	1	—	8	100.0	8	M	P
<i>Oxyjulis californica</i>	1	—	3	100.0	3	M	P
<i>Paralichthys californicus</i>	1	—	5	100.0	5	MI	P
<i>Syngnathus leptorhynchus</i>	1	—				R	LB
Unidentified fish larvae	49	1.3					
Total	3645						

collected in 44 samples. Mean monthly densities of larvae at the harbour entrance station were 0-1830 per 1000 m³ (overall mean = 380 per 1000 m³; S.E. = 80). *E. mordax* (northern anchovy) was the most abundant species at this station, followed by *H. pretiosus-osmerid*, *G. lineatus* (white croaker), *L. armatus* (Pacific staghorn sculpin), and *C. ios* (arrow goby); these taxa comprised 87% of the catch.

Seasonal peaks in larval abundance generally were characterized by the occurrence of a single taxon. At the harbour entrance station, 73% of the larvae collected in winter 1975 were *H. pretiosus-osmerid*, and 91% collected in summer and fall 1975 were *E. mordax* [Figure 2(a)]. Less distinct peaks were produced by *L. armatus* in winter 1976 and by *G. lineatus* during fall of all years. It is notable that the deep water of the Monterey Submarine Canyon influenced species composition of larvae in the slough and harbour; larvae from the mesopelagic species *Stenobranchius leucopsarus* (northern lampfish) were collected at the harbour entrance and bridge stations in January, and one larval *Bathylagus ochotensis* (deepsea blacksmelt) was caught in March at the harbour entrance station.

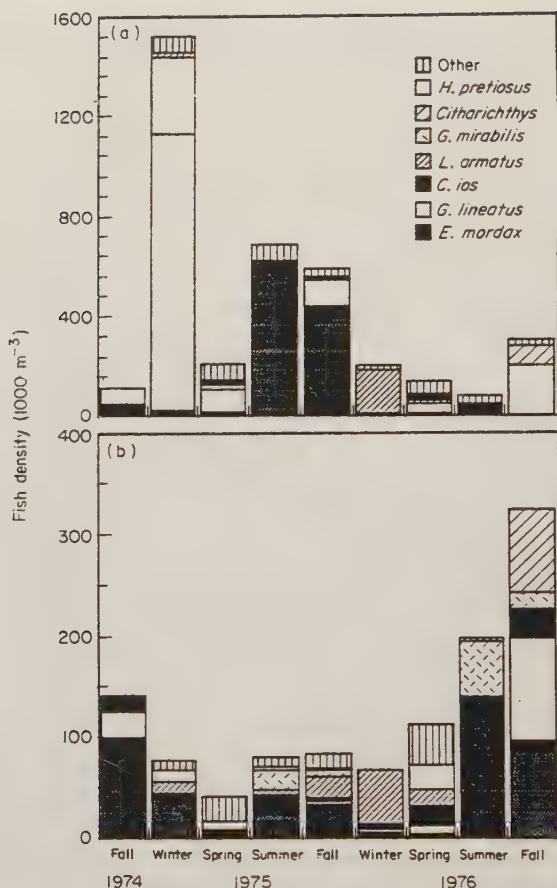


Figure 2. Seasonal average densities of dominant larval fish species collected at (a) the harbour entrance, and (b) the bridge stations in Elkhorn Slough from September 1974–September 1976.

Densities were lowest at the bridge station, ranging from 0 to 370 larvae per 1000 m³ (mean = 130 per 1000 m³; S.E. = 20). Sixteen species caught in 69 tows represented only 275 larvae. Eighty-nine percent of the total catch was comprised of *E. mordax*, *G. lineatus*, *C. ios*, *L. armatus*, *G. mirabilis*, *Citharichthys* spp. (sanddab) and *H. pretiosus*-osmerid, in rank order of abundance. The most prominent peak in abundance, representing *E. mordax* and *G. lineatus* larvae, occurred in late summer 1976 and early fall 1976 [Figure 2(b)]. Gobiid larvae (*G. mirabilis* and *C. ios*) also were present in large numbers during these periods. Newly hatched *Citharichthys* spp. larvae (S.L. = 2 mm) occurred in relatively high abundance (25% of catch) in early fall 1976 at both the bridge and harbour entrance stations.

Densities of larval fishes at the dairy stations also were low, ranging from 10 to 450 per 1000 m³ (overall mean = 200; S.E. = 20). From 70 tows, 261 larvae and 15 taxa were

identified. Peak abundance occurred in late summer and fall [Figure 3(a)], largely due to high numbers of *E. mordax* and *G. mirabilis*, and in winter 1976 due to *G. lineatus*, *E. mordax*, and *L. armatus*.

Overall density of larvae at the red house station was higher than at the bridge and dairy stations (mean = 290 per 1000 m³; S.E. = 50). Average monthly densities ranged from 10 to 1650 fish per 1000 m³. Twelve taxa were identified from 790 larvae collected in 70 tows. Ninety-one percent of the catch comprised four species (*G. mirabilis*, *C. ios*, *E. mordax*, and *L. armatus*); nearly 70% of all larvae were gobiids. Densities were highest in fall 1974 and in summer and fall 1976 [Figure 3(b)], largely because of *G. mirabilis*. *E. mordax* larvae also contributed to the high densities in fall. *L. armatus* and *C. pallasii* (Pacific herring) were seasonally abundant in winter and spring, respectively. *C. ios* larvae occurred in every season, with greater abundance in summer and fall.

Abundance of larval fishes was highest at the Kirby Park station (monthly mean densities were from 15 to 4000 per 1000 m³; overall mean = 770, S.E. = 130). Number of larval taxa, however, decreased with distance from the ocean, with only 12 taxa (one to six per tow) representing 1818 larvae at the Kirby Park station. Larvae of *G. mirabilis*, *E. mordax*, *C. ios*, and *C. pallasii* accounted for 93.3% of the total catch. Peaks in abundance [Figure 3(c)] primarily were due to *C. pallasii* larvae in spring, *E. mordax* in spring and fall, and large numbers of *G. mirabilis* in summer and fall (especially in September 1976 with 3520 larvae per 1000 m³). *C. ios* were present in substantial numbers throughout the sampling period.

Species similarity

Two distinct assemblages of larval fishes were discerned using percentage similarity index and Spearman's rank correlation coefficient (Table 2). Assemblages at the red house and Kirby Park stations, the two furthest from the ocean, were most similar to each other (PSI = 0.81; $r_s = 0.95$, $P < 0.01$). A high degree of similarity was indicated by both indices when evaluating pairwise comparisons of species composition between the harbour entrance, bridge, and dairy stations. Species composition at stations nearest the ocean (harbour entrance and bridge) was least similar to that of assemblages furthest inland. Species comparisons between the mid-slough dairy station and either the red house or Kirby Park stations were not as conclusive. Although the rank order of species abundance was significantly similar in these comparisons, PSI values were low. This indicated that the relative abundance of individual species differed between middle and upper areas of the slough, likely due to the dominance of *G. mirabilis* at the red house (57%) and Kirby Park (52%) stations (compared to 10% at the dairy station).

Size of larvae

Most larvae were relatively small and varied little in size (Table 1). *E. mordax*, *C. pallasii*, and *H. pretiosus*-osmerid had the broadest temporal or spatial size ranges. Size composition of *E. mordax* larvae varied significantly (Kruskal-Wallis; $P < 0.01$) among stations (Figure 4). Most *E. mordax* collected at the stations closest to the ocean were less than 15 mm S.L., and the smallest larvae (<5 mm S.L.) were abundant from June to September. *E. mordax* larvae were larger (up to 34 mm S.L.) at upper slough stations (red house and Kirby Park), and increased in length from June (3–6 mm S.L.) to March (19–32 mm S.L.). Young anchovies of the previous year class were no longer collected in plankton nets after the late spring and early summer at any station.

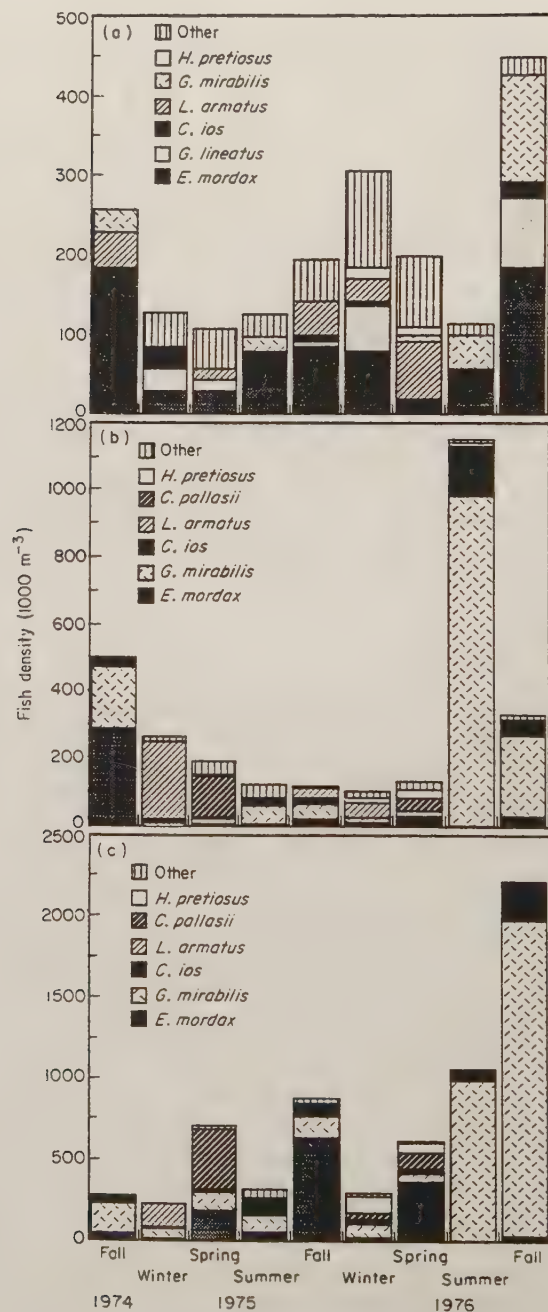


Figure 3. Seasonal average densities of dominant larval fish species collected at (a) the dairy, (b) the red house and (c) the Kirby Park stations in Elkhorn Slough from September 1974–September 1976.

TABLE 2. Bivariate Spearman's rank correlation coefficients (R_s , lower left matrix) and percentage similarity indices (PSI; upper right matrix) for species composition of larval fishes from five stations in Elkhorn Slough

	Harbour entrance	Bridge	Dairy	Red House	Kirby Park
	PSI				
Harbour entrance	—	0.71	0.61	0.29	0.41
Bridge	0.75**	—	0.80	0.44	0.49
R_s Dairy	0.59*	0.62*	—	0.48	0.54
Red house	0.41	0.41	0.80**	—	0.81
Kirby Park	0.39	0.38	0.69**	0.95**	—

*Significant at $P=0.05$; **significant at $P=0.01$.

Size composition of *H. pretiosus*-osmerid larvae also revealed a spatial trend of larger larvae (range = 25–48 mm; median = 32 mm S.L.; $n=60$) at the Kirby Park station and smaller larvae (range = 3–6 mm; median = 4 mm S.L.; $n=117$) at lower slough stations (harbour entrance and bridge). *Clupea pallasii* larvae also had a broad range of lengths (3–28 mm S.L.; Table 1), and were abundant primarily at the Kirby Park station, where they ranged in size from 5–28 mm S.L. (median = 18 mm; $n=66$).

Eggs

The 201 samples, which were collected from October 1975 to September 1976, included 24 085 fish eggs. Ninety-four percent of the eggs were from seven taxa, including *E. mordax* (57% of total abundance), *Citharichthys* spp. (19.8%), *G. lineatus* (6%), *Pleuronichthys verticalis* (hornyhead turbot), *P. coenosus* (C-O turbot), *P. decurrens* (curlfin turbot), and *Symphurus atricauda* (California tonguefish). The remaining 6%, largely 1 mm diameter eggs without oil globules (likely to be from the pleuronectid complex) and indistinguishable eggs of various sizes, were placed into the 'other' category. Only four taxa of eggs were collected also as larvae (*E. mordax*, *Citharichthys* spp., *G. lineatus*, and *P. verticalis*), of which two (*E. mordax* and *G. lineatus*) were among the eight most abundant larvae.

Density was highest in summer, largely because of numerous eggs of *E. mordax* at the three most seaward locations (Table 3). *E. mordax* eggs essentially were absent from the slough in winter and spring (November–April). In general, fish eggs were most abundant at the bridge station, decreasing dramatically in number toward the upper slough (the red house and Kirby Park stations). Eggs of *Citharichthys* spp. were collected year-round throughout the slough, with high abundance in summer and fall at lower slough stations (harbour entrance and bridge). Density of *Citharichthys* spp. eggs peaked later (October) at upper slough locations, exceeding that of *E. mordax*. Eggs of *G. lineatus* also were collected throughout the slough, but in relatively high numbers only at the two stations closest to the ocean; peak abundance occurred in fall and early winter, with few eggs found

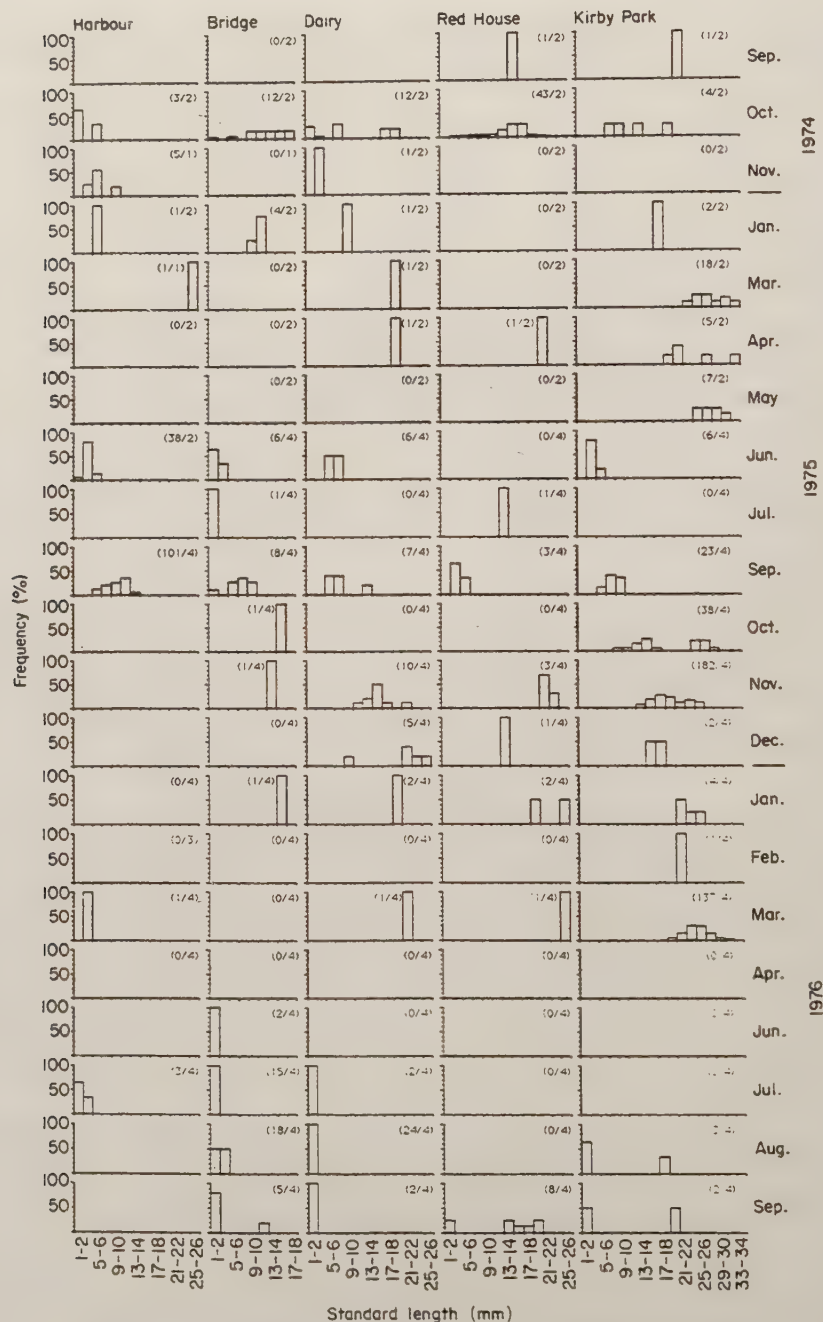


Figure 4. Length-class frequency distributions of *Engraulis mordax* larvae collected at five locations within Elkhorn Slough, CA; number of larvae/number of samples are shown.

TABLE 3. Seasonal average density (number per m³) of fish eggs collected at five locations in Elkhorn Slough, CA

Station/taxa	Fall	Winter	Spring	Summer
Harbour entrance				
<i>Engraulis mordax</i>	0.6	—	0.1	9.4
<i>Genyonemus lineatus</i>	0.7	—	0.4	—
<i>Citharichthys</i> spp.	1.7	T	0.1	2.7
<i>Pleuronichthys</i>				
<i>verticalis</i>	—	—	T	T
<i>P. coenosus</i>	—	T	T	T
<i>P. decurrens</i>	—	—	T	—
<i>Symphurus atricauda</i>	0.1	—	—	T
Others	2.0	T	0.1	2.7
Total	5.1	0.1	0.7	14.9
Bridge				
<i>Engraulis mordax</i>	5.1	T	0.1	26.8
<i>Genyonemus lineatus</i>	0.9	0.8	0.6	—
<i>Citharichthys</i> spp.	2.0	0.3	0.1	4.8
<i>Pleuronichthys</i>				
<i>verticalis</i>	0.1	T	T	0.1
<i>P. coenosus</i>	—	—	T	T
<i>P. decurrens</i>	T	—	—	—
<i>Symphurus atricauda</i>	T	—	—	—
Others	1.7	T	0.1	1.9
Total	9.8	1.1	0.9	33.6
Dairy				
<i>Engraulis mordax</i>	4.5	T	T	12.1
<i>Genyonemus lineatus</i>	0.4	0.5	0.1	T
<i>Citharichthys</i> spp.	3.3	1.3	0.3	2.6
<i>Pleuronichthys</i>				
<i>verticalis</i>	T	T	—	T
Others	1.7	T	T	1.1
Total	9.9	1.9	0.4	15.8
Red House				
<i>Engraulis mordax</i>	0.3	—	—	0.4
<i>Genyonemus lineatus</i>	T	0.1	T	—
<i>Citharichthys</i> spp.	1.5	0.3	0.3	0.1
Others	T	T	T	0.1
Total	1.9	0.4	0.3	0.6
Kirby Park				
<i>Engraulis mordax</i>	0.1	—	—	0.1
<i>Genyonemus lineatus</i>	T	T	—	—
<i>Citharichthys</i> spp.	0.3	0.2	0.1	0.2
Others	—	T	—	—
Total	0.4	0.2	0.1	0.3

A trace density (T) is less than 0.1 per m³; — means no eggs of that species were collected.

after March. *Pleuronichthys* spp. eggs had no seasonality, occurring in small numbers only at lower slough stations. Very low numbers of *S. atricauda* eggs were collected in summer and fall only at seaward stations.

Reproductive specialization

Six larval fish species were classified as resident (Table 1), of which five have demersal eggs and one [*Syngnathus leptorhynchus* (bay pipefish)] is live-bearing. Greater than 69%

of the total number of larvae were from demersal eggs; 56% of the larval abundance was classified as slough resident. Six species, and nearly 35% of the total abundance, were from marine immigrant adults. Fifteen species, representing < 7% of the total abundance, were considered to be of marine origin.

Discussion

There are similarities in species composition among Elkhorn Slough larval fish assemblages and those described in the few comparable studies of other west coast estuaries. Gobiid and clupeoid larvae dominated the catch in most systems. *Lepidogobius lepidus* (bay goby) and *C. pallasii* were analogous to *G. mirabilis* and *E. mordax* (the two dominant species in Elkhorn Slough), and accounted for 82% and 90% of all larvae collected in Humboldt Bay (California's northernmost estuary; Eldridge & Bryan, 1972) and Yaquina Bay, Oregon (Percy & Myers, 1974), respectively. *L. armatus*, *C. ios*, and osmerid larvae similarly contributed to the assemblages in Humboldt Bay (13% of the catch) and Elkhorn Slough (21.4%). *L. armatus* and *H. pretiosus* also were relatively abundant in Yaquina Bay. Ichthyoplankton assemblages of almost all southern California bays and estuaries are dominated by engraulid eggs (*Anchoa* spp.) and gobiid larvae (McGowen, 1977; Leithiser, 1981; Nordby, 1982; Horn & Allen, 1985). Numerical importance of engraulid larvae [*Anchoa* spp. (18.5%) and *E. mordax* (9.6%)] was second only to gobiids (38.8%) in upper Newport Bay (Horn & Allen, 1985). Sciaenid larvae were abundant only in Elkhorn Slough (*G. lineatus*) and bays to the south.

The limitations of ichthyoplankton surveys should be considered when describing habitat use by fishes. The number of egg and larval taxa collected in Elkhorn Slough is limited by species identification (e.g. taxonomic problems with larval gobiids, atherinids, and *Sebastes* spp.). Of the 32 taxa of fish eggs and larvae collected in Elkhorn Slough, eight were considered common (each representing > 1% of the total catch). Sixty-five species of juvenile and adult fishes have been collected in the slough, of which 40 have abundances > 1% of the catch at any one station (Yoklavich et al., 1991). Underestimates of the number of taxa and densities of individuals also result from avoidance of gear by larger larvae during daytime sampling and extrusion of small newly-hatched larvae. We expected to minimize avoidance by operating a pushnet without preceding bridles in relatively shallow (2–5 m) turbid (0.5–4.5 m visibility) water. Sampling at night could increase total numbers of some species, especially the already-abundant gobiids (Leithiser, 1981; Whitfield, 1989). Although the main channel of Elkhorn Slough is shallow and well-mixed, especially seaward of the tidal prism (Broenkow, 1977), the pushnet was limited to the upper 1-m of the water column and therefore inadequate for sampling epibenthic and shallow tidal creek habitats. Samples of juvenile fishes from tidal creeks of Elkhorn Slough (Yoklavich et al., 1991) comprised species that also were abundant in the ichthyoplankton survey (*E. mordax*, *L. armatus*, and the gobiids), but the second most abundant species (*A. affinis*) only ranked tenth in ichthyoplankton samples.

Reproductive specialization (i.e. egg type and spawning origin of adults) also influences descriptions of fish assemblages from egg and larval surveys. Adhesive, demersal eggs are common to resident fishes of Elkhorn Slough and are not collected in plankton samples. Percy & Richards (1962) noted a predominance of larval fish species from demersal eggs in the Mystic River estuary, and suggested that this aided in retention of eggs within the system. This specialization assists in maintaining adult populations in areas of discontinuous habitat. Embiotocids (seven species of surfperch) are the most abundant

group of adult fishes in Elkhorn Slough (Yoklavich *et al.*, 1991). Because embiotocids are viviparous and extrude well-developed young, eggs and larvae are not available to ichthyoplankton surveys. Similarly, three species of viviparous marine *Sebastes*, which release larvae offshore, were collected only as juveniles in otter trawls at near ocean stations (Yoklavich *et al.*, 1991). The young of several species of viviparous elasmobranchs, classified as partial-residents, also are not sampled with ichthyoplankton gear.

Two seasonal groups of larvae are distinguished from ichthyoplankton samples in Elkhorn Slough. *E. mordax* and gobiids (*G. mirabilis* and *C. ios*) form a late-summer and early-fall group. *E. mordax* were abundant also in winter, but these were mainly post-flexion larvae and early juveniles that were overwintering at the Kirby Park station. Both dominant gobiids have protracted spawning seasons (from February to September) that peak in late summer (Weisel, 1947; Prasad, 1948). Abundance of gobiid larvae increased with rising water temperatures throughout the slough, reaching maximum densities at 18–20 °C for *C. ios* and 19–23 °C for *G. mirabilis*.

Although some spawning of *E. mordax* occurs in coastal waters throughout the year (Ahlstrom, 1966), the central California subpopulation (offshore from San Francisco Bay to Point Conception) has a broad spawning peak from February to April (Parrish *et al.*, 1985), when mean water temperature is 14–16 °C (Smith & Lasker, 1978). Peak spawning of the northern subpopulation off Oregon and northern California is later (mid-June to mid-August), and at similar water temperatures (Richardson, 1980). Size distributions of larval *E. mordax* and spatial and temporal patterns of egg densities in Elkhorn Slough indicate that spawning occurs primarily at lower slough stations or in adjacent bay water in summer and early fall (July through August). A narrow band of warm (> 14 °C) water persists along the eastern edge of Monterey Bay, adjacent to Elkhorn Slough, beginning about July (Breaker & Broenkow, 1989), and coincides with our largest catches of *E. mordax* eggs in lower slough areas. Most *E. mordax* larvae were collected in slough water from 14 to 18 °C. This is similar to peak spawning in San Francisco Bay (from July–September) when mean water temperatures are 19–19.8 °C (McGowan, 1986).

While more speciose, a winter and early-spring group that included *L. armatus*, *H. pretiosus*-osmerid, two species of the silverside family Atherinidae, and *A. hexapterus* (Pacific sandlance) was not as abundant as the summer–fall assemblage. The winter-spring group was more variable in occurrence; pulses of high numbers of preflexion osmerid and *A. hexapterus* larvae were collected in single tows. Although *C. pallasii* larvae were seasonally abundant in the upper areas of Elkhorn Slough in the spring, the lack of adequate spawning substrate, such as extensive *Zostera marina* (sea-grass) beds, potentially limits use of the lower slough as nursery habitat. Submerged aquatic vegetation is relatively sparse in Elkhorn Slough, except for dense *Salicornia virginica* (pickleweed) in the intertidal marsh zone (1.8 m above MLLW) of the upper slough. Recent restoration of seagrass beds in Elkhorn Slough could modify distribution and enhance recruitment for those species with demersal, adhesive eggs.

The temporal occurrence of *G. lineatus* larvae in Elkhorn Slough corresponded to their spawning season from late-fall to spring off southern California (Goldberg, 1976; Watson, 1982), and to the presence of eggs from fall through spring at stations closest to the ocean. All *G. lineatus* larvae were very small (2–4 mm) and abundant only at locations west of the tidal prism, suggesting transport from the slough during early development. Most *G. lineatus* larvae in southern California were collected in coastal water within 4 km from shore (Watson, 1982).

Seasonal patterns of larval fish abundance were similar in many of the west coast studies of inshore larval fish assemblages. Peak abundance of all larvae in Yaquina Bay, Oregon occurred in winter and spring, largely due to high numbers of *C. pallasii*; highest densities of the co-dominant *Lepidogobius lepidus* occurred in summer. In Humboldt Bay, California high larval abundances in January–February and in April–May were produced by species that formed the winter–early spring group in Elkhorn Slough (Eldridge & Bryan, 1972). Because Humboldt Bay did not have large populations of larval *E. mordax* or *G. mirabilis*, a summer–fall increase in abundance was not obvious; however, the number of *C. ios* increased in October. Highest numbers of larval fishes occurred in May and September in southern California's upper Newport Bay, largely due to *Anchoa* spp., *E. mordax*, *C. ios*, and other gobiids (Horn & Allen, 1985).

Preflexion larvae of pleuronectiform fishes essentially were absent from Elkhorn Slough, Humboldt Bay (Eldridge & Bryan, 1972), and Yaquina Bay (Pearcy & Myers, 1974). However, one large pulse of newly-hatched *Citharichthys* spp. larvae was sampled in September 1976 at the three stations closest to the ocean in Elkhorn Slough, and *Citharichthys* spp. eggs were found at all times of year throughout the slough in relatively high numbers. Newly-settled juvenile flatfish [e.g., *Parophrys vetulus* (English sole), *Citharichthys stigmaeus* (speckled sanddab), and *Platichthys stellatus* (starry flounder)] can be abundant in the three embayments (Horn & Allen, 1976; Boehlert & Mundy, 1987; Yoklavich et al., 1991). *Parophrys vetulus* spawn offshore, and metamorphosing larvae (about 15–23 mm S.L.) recruit to bays and estuaries (Boehlert & Mundy, 1987). Boehlert & Mundy (1988) suggested that physical and behavioural factors that are related to tidal flux operate in the recruitment and retention of larval and juvenile fishes in estuaries. *Citharichthys* spp. and *P. stellatus* juveniles may recruit in a similar manner, although gravid *P. stellatus* have been collected in inshore areas that have little tidal flushing and in upper areas of tidal creeks in Elkhorn Slough.

The decrease in number of larval taxa with distance from the ocean occurs as well in other bays and estuaries. Fewer taxa were collected at Humboldt Bay's most inland stations, which had higher variability in temperature and freshwater input (Eldridge & Bryan, 1972). Number of taxa was maximum at the mouth of Yaquina Bay and decreased up the estuary (Pearcy & Myers, 1974). In Elkhorn Slough, greater seasonal fluctuations in water temperature and salinity occur at upper slough stations (red house and Kirby Park; Figure 5), potentially limiting the number of taxa able to utilize this area either as spawning or nursery grounds. Marine species, such as *G. lineatus*, *A. hexapterus*, *Sebastes* spp., and most flatfishes, spawn offshore. When these larvae, and in some cases eggs, occur in the slough, it is primarily in the lower slough, undoubtedly transported onshore by surface currents.

The occurrence of larvae of the deep-dwelling fishes *Stenobranchius leucopsarus* and *Bathylagus ochotensis*, categorized as offshore species (Boehlert et al., 1985), was not unexpected in samples from the harbour entrance station during winter and early spring, because net flow of water over Monterey Submarine Canyon is believed to be up-canyon (onshore) most often (Breaker & Broenkow, 1989). Larvae of mesopelagic species also were collected at the mouth of Humboldt Bay (Eldridge & Bryan, 1972) and in Yaquina Bay during the winter period of onshore transport (B. C. Mundy & G. W. Boehlert, unpubl. data).

Although inland slough regions had fewer taxa, they contributed the greatest numbers of individual larvae. Resident gobiids were the most abundant larvae in the slough; their rank abundance increased with distance from the harbour entrance. Adults and juveniles

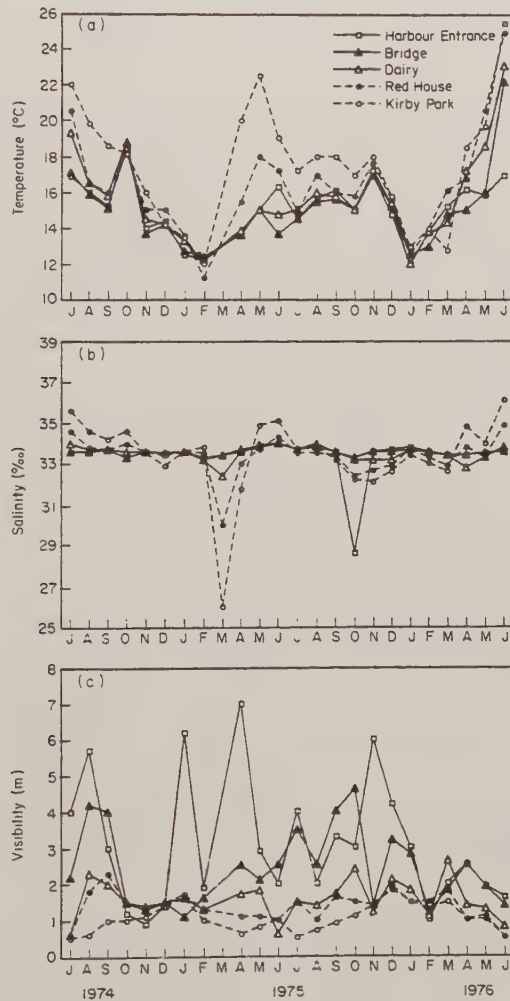


Figure 5. Average monthly water (a. temperature, (b) salinity, and (c) visibility at five locations in Elkhorn Slough, CA from July 1974 to June 1976 [data from Broenkow (1977)].

of *G. mirabilis* and *C. ios* were collected almost entirely in tidal creeks and inland slough regions (Barry, 1983; Yoklavich *et al.*, 1991). Mudbanks and extensive *Salicornia* spp. beds bordering these regions provide suitable habitat for spawning gobiids.

Along with localized spawning habits of adults, hydrographic conditions in Elkhorn Slough contribute to the dominant spatial patterns in abundance of fish eggs and larvae. Significant differences between lower (harbour entrance and bridge) and upper (red house and Kirby Park) slough assemblages suggest that the tidal prism (about 4.8 km from the harbour entrance) assists in retaining some species within the slough. Elkhorn Slough

receives little freshwater runoff, except during winter months of non-drought years. Mid-slough (dairy; 3.1 km from harbour entrance) species composition was in transition between lower and upper groups. Water is exchanged daily by tidal currents, and seasonal variations in temperature and visibility are similar at harbour entrance, bridge, and dairy stations (Figure 5; Broenkow, 1977). The most abundant larvae at these stations were very small preflexion *E. mordax* and *H. pretiosus*-osmerid, both classified as marine immigrants. Newly hatched *G. lineatus*, a marine species with pelagic eggs, also was abundant at the most seaward stations, suggesting advection of eggs and larvae into the slough rather than spawning *in situ*. The water mass to the east of the tidal prism (red house and Kirby Park stations) fluctuates widely in temperature and salinity, and has lower visibility (Figure 5). Newly hatched *E. mordax* are distributed progressively eastward to the Kirby Park station, and seemingly thrive in the shallow upper slough, as indicated by increased length distributions from September to March. Zooplankton samples collected in a 135 µm mesh net concurrently with the larval fishes at the upper slough stations in late spring, summer, and early fall contained high densities of potential prey, such as barnacle nauplii, polychaete larvae, and all stages of the copepods *Acartia* spp. and *Oithona spinifera* (Cailliet et al., 1977; Pace, 1977). The high water residence time (greater than 300 days; Smith, 1973), and increased summer water temperatures (Figure 5), potential zooplankton prey densities, and available substrate for adhesive demersal eggs in shallow inland marsh habitats of the slough enhance reproductive success, larval retention, and survival.

From earlier studies of juveniles and adult fishes (Barry & Cailliet, 1981; Yoklavich et al., 1991) and the present ichthyoplankton survey, the relatively small area of Elkhorn Slough serves as spawning and nursery grounds for several species of transient marine fishes and at least six species of resident estuarine fishes. Five of the ten most abundant species of larval fishes are of commercial importance, either directly (e.g. *E. mordax*, *C. pallasii* and *Citharichthys* spp.) or indirectly as forage for other commercial species (e.g. osmerids and atherinids). While Elkhorn Slough's contribution to nearshore fish assemblages is limited by size, the spatial and temporal patterns in larval fish abundance are important for further assessment of the linkage between inshore productivity and Monterey Bay.

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